Diets of Miocene proboscideans from Eurasia

and connections to environments and vegetation

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Tiivistelmä – Referat – Abstract

The Miocene epoch (c. 23-5 million years ago) was a noteworthy geological time period in which significant changes took place both in the climate regimes as well as in vegetation characteristics, bringing about novel adaptations in many herbivorous lineages. These adaptations constituted morphological, dietary, and ecological factors in a relatively short period of evolutionary time. Among these herbivores were the proboscideans, the living and extinct elephants, which were among the most dominant and largest herbivores at the time. Despite that proboscideans were diverse and large group of hundreds of species, yet the understanding of dietary and ecological patterns of majority of Miocene sympatric species is still limited.

The aim of this study was to analyse the molar surfaces of Miocene proboscideans (e.g. *Deinotherium* and *Gomphotherium*) from Eurasia to provide a reconstruction of the feeding preferences of the study species based on observed dental wear. The dental wear indicates the abrasiveness of the diet, thus allowing broad categorization to either browser (<10% grass in the diet), mixed-feeder (10-90% grass in the diet) or grazer (>90% grass in the diet). Secondly, this study aimed for providing estimation of the environmental characteristic and vegetation patterns of the study localities by comparing to the previous studies and to hypsodonty value (proxy of general openness and aridity of the environment). Proboscidean dietary signals from the key localities of Maragheh (Iran) and Pannonian basin (Austria) were compared with the paleobotanical studies. Thus, the general estimation of spatial and temporal variation of the environment characteristics in the study localities were based on these parameters. The materials of fossilized molars were analysed by mesowear angle method, in which the measured angles show the diet abrasiveness due the nutritional targets' differences.

The results allowed the reconstruction of the feeding preferences which suggested that majority of Miocene proboscideans were browsers and browse-dominated mixed feeders or pure mixed-feeders. Instead, *Choerolophodon pentelici* was found grass-dominant mixed-feeder. The wide spectrum of feeding preferences allowed diet flexibility according available vegetation and also these sympatric species to co-exist by niche partitioning. Thus, demonstrating clearly the connection between diets and environments thought the diet.

As a conclusion, in the diet of the paleocommunities of proboscideans had, on average, more grass-dominant components in open and dry environment likely due the presence of grass-dominant vegetation. Instead, in the wet conditions the closed-canopy forest environments enhanced browsing. Further, the results indicated shift in feeding preferences of proboscideans prior to Miocene climate and environment changes. These results are in line with the findings of the previous studies of modern elephants' diet-environment relationships. The further studies would provide insight to the relative amounts of the grass in the diet of Miocene proboscideans.

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Proboscideans Miocene Grazer Mesowear Paleoecology

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Mioseenikauden norsueläinten ravinto sekä sen yhteys ympäristöön ja kasvillisuuteen.

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Tiivistelmä – Referat – Abstract

Mioseeniepookki (n. 23 – 5 miljoonaa vuotta sitten) oli merkittävä ajanjakso, jonka aikana ilmastossa ja kasvillisuudessa tapahtui mullistavia muutoksia, jotka aikaan saivat uusia sopeutumia monissa kasvinsyöjissä. Sopeutumat koskettivat niin morfologisia, ruokavaliollisia kuin ekologisia tekijöitä evolutiivisesti varsin lyhyessä ajassa. Näistä kasvinsyöjistä eräitä merkittävimpiä olivat norsueläimet, jotka olivat nykyistä suurempi ja ekologisesti monipuolisempi ryhmä. Mioseeniepookki oli merkittävä käännöskohta näiden norsueläinten evoluutiossa, jonka aikaisesta lajien ravintokäyttäytymisestä sekä ekologiasta tiedetään varsin vähän.

Täten tämän tutkimuksen kohteena olivat Euraasian muinaiset norsueläimet (Proboscideans) muun muassa *Deinotherium* ja *Gomphotherium*- suvut. Työn tarkoituksena oli tutkia mioseeniepookin norsulajien fossilisoituneita hammaspintoja, joiden kuluminen signaloi niiden ravinnosta sekä arvioida näiden lajien elinympäristöjä vertaamalla saatuja tuloksia olemassa olevii n aineistoihin aikakauden kasvillisuuden ominaispiirteistä sekä ilmastohistoriasta. Aineistona olivat tutkimuslajien poskihammasfossiilit mioseenikauden löytöpaikoilta. Saatua aineistoa verrattiin hypsodontia arvoon, joka kertoo ympäristön suhteellisesta avoimuudesta ja kuivuudesta. Lisäksi kahta keskeisimmäksi havaittua löytöpaikkaa; Maraghehin (Iran) ja Pannonian altaan (Itävalta) aineistoa verrattiin aikaisempiin kasvillisuustutkimuksiin. Täten voitiin arvioida kasvillisuuden rakennetta sekä sen temporaalista ja spatiaalisesta vaihtelua perustuen hampaiden kulumiseen. Menetelmänä käytetiin mesowear angle-analyysia missä poskihampaista mitatut taittokulmat kertovat ravinnon aikaansaamasta kulumisesta.

Havaitun poskihampaiden kulumisenasteen perusteella voitiin määritellä tutkimuslajien ruokavalio. Tutkimuksen perusteella valtaosa mioseeniepookin norsueläimistä olivat lehdensyöjiä sekä lehdensyöntiin painottuvia sekasyöjiä tai puhtaasti sekasyöjiä. Erikoistuneeseen heinänsyöntiin painottui yksi tutkimuslaji; *Choerolophodon pentelici*. Ravinnon monipuolisuus mahdollisti ruokavalion joustavuuden saatavilla olevan kasvillisuuden sekä näiden suurten kasvinsyöjien esiintymisen samalla alueella ekolokerojen eroavaisuuden myötä. Tutkimus osoitti selkeän suhteen lajien morfologian ja ympäristön välillä ruokavalioiden ominaispiirteiden kautta.

Täten norsueläinyhteisöjen ruokavaliot olivat pääsääntöisesti heinävaltaisempia kuivemmissa sekä avoimemmissa ympäristöissä, jossa heinävaltaisen kasvillisuuden osuus oli todennäköisesti suurempi. Vastavuoroisesti kosteammissa metsäympäristöissä lajit suosivat lehdensyöntiä. Tulokset antoivat viitteitä norsueläinten ruokavalioiden painopisteen siirtymisestä lehdensyönnistä kohti heinävaltaisempia ruokavaliota, vasteena mioseeniepookin ympäristötekijöiden sekä ilmasto-olosuhteiden muutoksiin. Tutkimustulokset tukevat aikaisempien tutkimusten löydöksiä nykynorsujen ravinnon sekä kasvillisuuden rakenteen suhteesta. Jatkotutkimukset tarjoaisivat selkeän todisteen heinäkasvillisuuden määrällisestä osuudesta mioseenikauden norsueläinten ravinnossa.

Avainsanat – Nyckelord – Keywords

Norsueläimet Mioseeni Heinänsyönti Mesowear Paleoekologia

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1 INTRODUCTION

The Cenozoic era, the Age of Mammals, experienced multiple rapid and gradual changes in climate and environment conditions during its 65 million-year history (Blois & Hadly, 2009; Janis, 1993; Strömberg & McInerney, 2011). Especially changes in vegetation influenced the evolution and ecology of many herbivorous mammalian lineages (Janis, 2008). Their most abundant representatives were ungulates (hooved animals) and proboscideans (elephants and their relatives), which were the dominant and largest herbivores in terrestrial ecosystems at the time (Janis, 2008; Saarinen, 2008). Especially during the Neogene period (23 – 2 Ma= mega-annum, millions of years) the global cooling and spreading of grasslands was a significant turning point in ungulates' evolution (Blois & Hadly, 2009; Janis, 1993). Subsequent to Neogene climate change the evolutionary trend led in many ungulate groups to the gradual shift in feeding adaptations from browsing (feeding on dicotyledonous leaves and branches) to different degrees of grazing i.e. feeding on grass (Janis, 1993; Saarinen, 2008; Strömberg & McInerney, 2011).

The Neogene climate change induced in Eurasia a transformation of previously lush, closed forest into drier and more open grasslands and woodlands, especially in the Mediterranean region (Eronen et al., 2010; Janis, 1993). Thus, this significant change in environment, necessitated among other morphological changes a dentition that could utilize the new type of dominant food source; grass (Fortelius et al., 2002; Janis, 2008). Due to its high phytolith (i.e. particles of opal silica) content, grass has been found to be highly abrasive on tooth enamel (Damuth & Janis, 2011; Lucas et al., 2014; Saarinen, 2008). Thus, during the Neogene period in many grass-eating mammal lineages, the dentition increased in complexity and in height of the molar, optimizing it for cutting and shearing tough food items (e.g. grass) and posing higher resistance against dental wear. (Damuth & Janis, 2011; Janis, 2008; Janis & Fortelius, 1988). These evolutionary processes have resulted in specialized dentition that is divided into multiple different cheek teeth patterns, each of which vary in their occlusal surface (i.e. working surface of the molar) complexity and thus in functional properties with the mechanical properties of the food the species has evolved to utilize (Göhlich, 1999; Ungar, 2015; von Koenigswald, 2018).

Ungulates, having a long evolutionary history throughout the Cenozoic era with high species richness distributed globally both in extant and extinct taxa, have long been in focus of ecological and palaeontological studies (Janis, 2008; Kaiser & Schulz, 2006; Mendoza, Janis, & Palmqvist, 2002; Saarinen, 2019). Especially, modern ungulates have been studied extensively, not only in terms of ecology but also

for taxon-specific dietary adaptations, morphologies and behaviour (Fraser & Theodor, 2011; Janis, 1988, 2008; Pérez-Barbería & Gordon, 2001). Based on these findings, the feeding adaptations of modern ungulates fall into three broad categories; grazers (>90% of grass in a diet), mixed feeders (10 - 90% of grass) and browsers (<10% of grass) (Fortelius & Solounias, 2000; Hofmann & Stewart, 1972). In addition to grass, ungulates utilize woody and non-woody dicotyledonous plants e.g. leaves, shoots, tree bark, and shrubs (Saarinen, 2019). However, these simple generalizations include a vast continuum of species ranging from those exclusively feeding on grass to those utilizing hardly any (Rivals & Lister, 2016; Saarinen & Lister, 2016). Thus, feeding adaptations discuss the foods species is capable of utilizing, not the actual diet *per se*. Moreover, the diet within species, and in some extent within populations, includes significant variation according to available vegetation, the openness of the habitat, and presence of competing herbivores (Rivals & Lister, 2016; Saarinen & Lister, 2016).

Understanding of modern ungulates' diets has provided a quantitative way to determine craniodental characteristics that are associated with feeding adaptations (Janis, 1995; Mendoza et al., 2002). These studies have indicated that species with different diets have measurable differences in morphologies as well. Based on recent studies, many morphological aspects such as skull shape, mandible size and dentition characteristics are found to correlate with feeding adaptations (Fortelius, 1985; Mendoza & Palmqvist, 2008; Semprebon, Janis, & Solounias, 2004). For instance, grazers tend to have more complex dentition accommodated with deeper mandible expressing more abrasive diet, than browsers (Janis, 1995; Saarinen, 2019).

Especially ungulates molars and premolars have been identified to be useful dietary indicators as they preserve the contact with diet components (Ackermans, 2020; Saarinen et al., 2015). Evolutionary history has shaped the dentition according to the feeding adaptations that is referred to as primary morphology of the tooth (Saarinen et al., 2015). However, after tooth eruption, the primary morphology reforms subsequently to dental wear alone, which gradually modifies occlusal surfaces into distinctive shapes referred as secondary morphology (Saarinen et al., 2015). Tooth wear results directly from the main purpose of the teeth; acquiring and mechanical grinding of the food (von Koenigswald, 2018). In herbivores the key function of teeth is to rupture cellular walls of the plant material during mastication in order to release the nutrients that otherwise would pass through undigested (Ungar, 2015). Thus, dental wear is caused by different nutritional targets and thus preserves food preparation (abrasion) and mastication (attrition), that are discussed in more detail in Section 5.2. Hence, studying teeth can reveal much about species feeding preferences (the food species actually utilize) and ecology (Mendoza et al., 2002).

These correlations found in modern ungulates' diets and morphologies have provided a comprehensive foundation for the study of analogies in extinct ungulates (Mendoza et al., 2002; Saarinen & Lister, 2016;

Ungar, 2015). Thus, in paleoecological studies, the fossils provide information about the biotic and abiotic relationships of extinct species (Kaiser & Schulz, 2006; Kaiser et al., 2013; Su & Croft, 2018). Today, increasing interest is focused on reconstructing past mammal communities (Calandra et al. 2008; MacFadden, 2007), the habitats these species lived in (Kaiser & Schulz, 2006; Su & Croft, 2018) and the climatic regimes that influenced them (Fortelius et al., 2002; Kaiser & Rössner, 2007). According to previous studies, the structure of herbivorous communities in general reflects the vegetation patterns of the area as grazing and grass-dominant mixed-feeders are most abundant in grassland habitats while browsers and browse-dominated mixed-feeders are dominant in forest environments (Janis, 1993; Kaiser et al., 2013; Saarinen & Lister, 2016). Consequently, recent studies have also shown correlation with high crowned, and thus wear resistant, teeth (termed as hypsodonty) with grazing in general which in turn is connected to open and arid environments (Damuth & Janis, 2011; Eronen et al., 2010; Janis, 1988; Kaiser et al., 2013; Mendoza & Palmqvist, 2008).

In light of these findings, the dietary analyses are important for paleoecological reconstructions (Calandra et al., 2008; Janis, 2008; Saarinen et al., 2015; Saarinen & Lister, 2016). Diet is the most studied variable in paleoecological research as it links fossilised morphology to ecology (Janis, 2008; Mendoza & Palmqvist, 2008). Ecomorphological comparison between living species known diet and morphology to extinct ungulate craniodental characteristics has been identified as a practical tool for illustrating feeding preferences of these species (Eronen & Rössner, 2007; Mendoza et al., 2002; Pineda-Munoz et al., 2017) . In previous studies, structural and functional adaptations of ungulates fossilised teeth have been recognized to perform well in palaeodietary reconstructions (Fortelius & Solounias, 2000; Mendoza et al., 2002; Saarinen & Karme, 2017).

The extent of modern ungulate-related studies have given insight to the question of how morphology varies with diet (Fraser & Theodor, 2011). As a result, a variety of dietary proxies have been introduced that record diet variation both in extant and extinct taxa (Fraser & Theodor, 2011). These include microwear (food induced microscopic scratches and pits on tooth enamel), hypsodonty value (the relative height of unworn tooth crown, the increase of which compensates heavy dental wear) and mesowear (dental wear induced occlusal shape and relief), that have been applied for reconstructing ecological and evolutionary patterns within and between taxa (Fortelius & Solounias, 2000; Fraser & Theodor, 2011; Mendoza & Palmqvist, 2008). However, these proxies indicate the diet in different temporal scales. Hypsodonty addresses a broad evolutionary time scale, while microwear offers insight to the final days of an individual (Davis & Pineda Munoz, 2016). In between these two extremes lies mesowear, which preserves traces of diet over the final months and in some cases, the entire lifetime (Davis & Pineda Munoz, 2016; Fortelius & Solounias, 2000), see Section 7.1.

This has generated an opportunity for paleontological reconstructions of extinct proboscideans (Calandra et al., 2008; Calandra et al., 2010; Rivals & Lister, 2016; Saarinen et al., 2015; Saarinen & Lister, 2016). During the Neogene period, proboscideans were a diverse group with hundreds of species (Shoshani & Tassy, 2005) which existed in a wide range of habitats and climate conditions (Göhlich, 1999). Especially during the Miocene epoch (23 - 5 Ma) changes in environmental conditions (as discussed in Section 3) had a diverse effect not only on geographical ranges and abundances of proboscideans, but also in the ecomorphology of these large mammals, further discussed in Section 4 (Saarinen, 2019; Shoshani & Tassy, 2005).

Morphologies, evolution, and distribution of proboscideans is well characterised (Göhlich, 1999; Loomis, 1936; Shoshani & Tassy, 1996, 2005). However, the paleoecological reconstructions of proboscideans are less common and have differentiating spatial and temporal scales (Fortelius & Solounias, 2000). For proboscidean related studies the mesowear method has been extended to the mesowear angle method, introduced by Saarinen et al. (2015), which is based on measuring the relief of worn molar surfaces as angle measurement for reconstructing diets of the species. In the study of Saarinen et al. (2015), the authors showed that the measured signal of dietary abrasiveness reflected the proportion of grass in the diet of Columbian mammoth (*Mammuthus columbi*) population from the Late Pleistocene (2,5 - 0,11 Ma) California. Furthermore, in a study of Saarinen & Lister (2016), the authors discussed Pleistocene proboscidean species of Britain from genera of *Mammut*, *Mammuthus*, *Anancus* and *Palaeoloxodon*. These taxa were found to be relatively flexible feeders with ability to prefer grazing but maintain browsing component according to available vegetation. By comparing with pollen records, the mesowear angle measurements specifically reflected the local vegetation patterns and utilizing grass rather than open ground feeding in general. Furthermore, microwear studies (Calandra et al., 2008, 2010) of two sympatric proboscideans families (*Gomphotherium* and *Deinotherium*), suggested differences in feeding preferences and niche partitioning in woodland habitats during the Miocene epoch (23 - 5 Ma). Results suggested browsing for *Deinotherium* and shifting mixed-feeding for *Gomphotherium* species.

Despite the extensive knowledge of all proboscideans' morphology and diets of more recent species, understanding of dietary and ecological patterns of the majority of extinct proboscideans is still limited. In view of this, this thesis discusses the Eurasian proboscidean community, constituting seven study genera (*Choerolophodon, Deinotherium, Gomphotherium, Konobelodon, Prodeinotherium, Tetralophodon* and *Zygolophodon*) and reaches further in the past to the significant turning point of proboscideans evolution of the Miocene epoch (ca. 23 - 5 Ma) with the background of paleoecological studies and understanding of ungulates ecomorphological correlations.

1.1 THESIS STRUCTURE

This thesis is structured in the following manner. In Section 2, I will provide the purpose of this study with two study goals. In Section 3 I will introduce the stratigraphic division of the Miocene epoch and the most essential characteristics of the climate and environments in Eurasia that faced significant changes during the epoch. In Section 4, is will establish the proboscideans order and summarize their responses to the changes discussed in the Section 3.

Next, Section 5 discusses the dental characteristics of proboscideans and the dental wear processes prior to the study methodology. In Section 6, I will establish the study species and their phylogeny based on representative differences in dentition. Furthermore, this section introduces the data collection practises from fossilised molar specimens, introduced in Section 5, continuing to constituting study localities around Eurasia.

In Section 7, Methods, I will establish the studying technique; the mesowear angle method, prior to differentiating the diets of the Miocene proboscideans based on dental wear on the molar specimens. Due to the recently introduced study methodology (Saarinen et al., 2015), I will demonstrate in Section 7.1 the measurement technique differentiating based on the diversity in the cheek teeth patterns. Thus, followed by calculations (Section 7.2) from different levels of a molar into proboscidean communities, required for further statistical analyses. Consequently, Section 8 will show the results of the diet characterization, the differences in proboscidean paleocommunities and the key characteristics of environment related data. Lastly, I will reflect the results against recent scientific literature in Section 9, from which the conclusions reached will be outlined in Section 10.

2 STUDY OBJECTIVES

The purpose of this study is to reconstruct the feeding preferences of the studied proboscidean genera. The first goal of this study is to analyse the dental wear signals of the occlusal surfaces of fossilized proboscidean molars, which indicate the abrasiveness of the diet of the species (Saarinen et al., 2015), and thus serve as a proxy for distribution to either browsing, mixed feeding, or grazing (Fortelius & Solounias, 2000; Saarinen et al., 2015). I will apply the mesowear angle method (Saarinen et al., 2015) to investigate connection between the feeding preferences and dental wear. Determined grazing - browsing gradient of proboscidean diets is hypothesized to provide insight to the Miocene epoch (23 - 5 Ma) environment characteristics in Eurasia.

The second goal of this study is to use the measured variation in dental mesowear as an ecometric tool for estimating the vegetation patterns and environment variables of study localities in Eurasia. The "ecometrics" refer to such traits measurable from fossil communities of organisms that are correlated with properties of the environmental conditions and climate under which the communities lived in, and are considered as nearly taxon-free trait distributions within these communities (see Fortelius et al., 2016; Kaya et al., 2018). In previous studies, the dental mesowear in proboscidean communities has been shown to correlate with vegetation structure despite differences in species composition (e.g. Cerling et al., 1999; Saarinen and Lister, 2016). Thus, it could be regarded as an ecometric variable that can be used for reconstructing environmental characteristics and vegetation composition of the Miocene. Under particular interest are habitat openness and the distribution of grass vegetation over the forest dominant vegetation, which ultimately contribute to climate (Eronen et al., 2010; Fortelius et al., 2016; Saarinen & Lister, 2016).

For better understanding of the paleoecology of sympatric proboscideans, I will discuss the results with temporal and spatial variation on population and community level, but also between localities distributed around Eurasia. Thus, this study aims to provide a window to the Miocene Eurasia, and to diets and habitats of extinct proboscideans. This thesis will be conducted in co-operation with the Department of Geosciences.

3 MIOCENE EPOCH – THE PERIOD OF MAJOR CLIMATE CHANGE

Evolutionary transitions of proboscideans can only be understood in the light of climate regimes and environment characteristics present in the Miocene epoch. Thus, in this section I will briefly describe the geological time-scale of the Miocene epoch and main changes in climate and environmental characteristics in the Europe and Western Asia, which impacts on distribution and feeding preferences of proboscideans will be described in later Section 4. The stratigraphic division of the Miocene epoch is presented in Figure 1 with temperature gradients, as discussed next.

The Miocene epoch extends from ca. 23 - 5,3 Ma and it is the first of two epochs in the Neogene period (ca. 23 - 2,5 Ma), followed by the Pliocene epoch of 5,3 - 2,5 Ma (Cohen et al. , 2013). The Miocene epoch has three sub-epochs of the Early (23 - 15 Ma), Middle (15 - 11 Ma) and Late (11 - 5 Ma) Miocene (Cohen et al., 2013). The Miocene epoch is further divided into European Land Mammal Zones (MN) defined by the evolutionary changes in mammals, their ranges and further by the representative characteristics of the taxa in certain time scale (Steininger, 1999). Thus, MN values are considered biostratigraphic units, that are valid from the Early Miocene onwards. In this study, MN time units are addressed equivalent to the Miocene

sub-epochs according to Fortelius et al. (2002) and Eronen et al. (2010). Thus, the Early Miocene composes the MN 1 – MN 5, followed by MN 6 – MN 8 of the Middle Miocene and respectively with MN 9 – MN 13 of the Late Miocene.

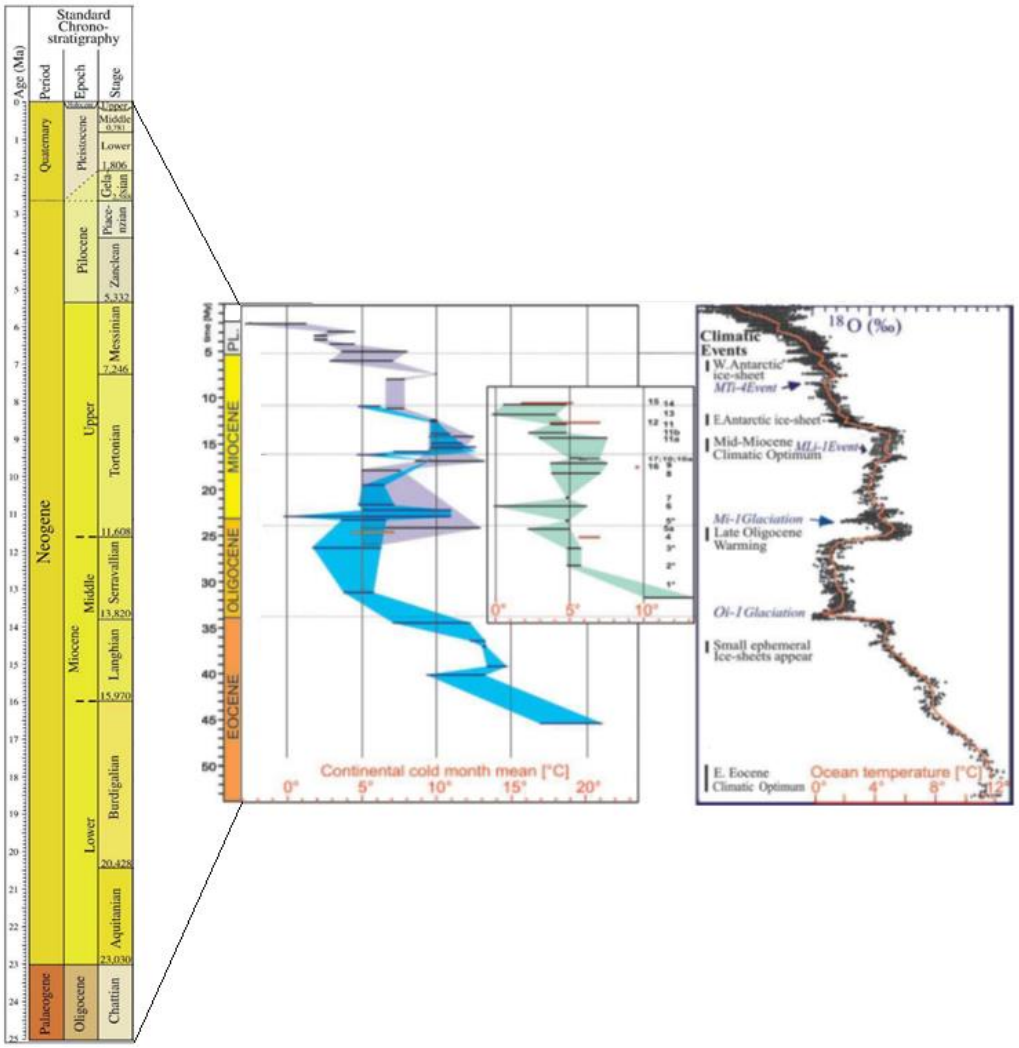


Figure 1. Stratigraphic subdivision of Neogene. The Miocene epoch and subdivision into the Early Miocene (Lower), the Middle Miocene and the Late Miocene (Upper) shown on the left. Modified according Ivanov et al. (2010). On the right (A.) continental temperature reconstruction (Mosbrugger, Utescher, & Dilcher, 2005) compared (B.) of ocean temperature gradient based on oxygen isotopes (Zachos, Pagani, Sloan, Thomas, & Billups, 2001).

The Miocene epoch is one of the interesting divisions of Cenozoic era as it was time of global changes in climate, environment and vegetation patterns with rise of modern fauna (Semprebon et al., 2004). The climate of the Miocene epoch was the last warm episode of the history following the greenhouse of the Oligocene and dropping towards the Pliocene and ultimately the ice age climate of the Pleistocene with the establishment of large Northern Hemisphere ice sheets (Ivanov et al., 2010). Several studies, which include both paleontological and geochemical studies, have documented the warm and humid conditions from the Early to the Middle Miocene (e.g. Eronen & Rössner, 2007; Ivanov et al., 2010; Janis, 1993). However, the Late Miocene was characterized with a continuous trend of decrease in temperature and precipitation,

resulting in increase of seasonality (Ivanov et al., 2010). This dramatical global temperature decline has been associated with development of more arid vegetation patterns as well as reduction mammalian taxonomic diversity at the end of the Miocene (Fortelius et al., 2002; Janis, 1993). However, the most staggering change was the rise of grasslands and the evolutionary changes it contributed. The general trends of Miocene temperature gradients are shown in Figure 1, which shows the similar patterns of decreasing temperatures in both of continental temperature reconstruction and ocean surface temperatures.

The begging of the Early Miocene, experienced similar conditions with the previous Oligocene epoch, indicating relatively warm and humid climatic conditions throughout Eurasia (Fortelius et al., 2002; Janis, 1993). According to paleobotanical proxies the Early Miocene had weak seasonality and in general precipitation between 800 - 1200 mm per year in Europe (Bruch et al., 2007; Mosbrugger et al., 2005). According to estimations by Eronen et al. (2010) based on fossil mammals ecomorphology, the precipitation in the Early Miocene had similar values in Central Europe, but more regional variation, especially in Mediterranean with estimations of precipitation only 300 - 700mm per year. The Western-Eurasia indicates generally warm and humid conditions based on ecomorphological proxies (see Fortelius et al., 2002). Furthermore, Ivanov et al. (2010) projected that mean annual temperatures between 16 - 18 °C. In general humid and warm conditions favoured life including tropical elements both in both in oceans and in land in European latitudes as high of 52 degrees north e.g. in regions of modern United Kingdom to Poland (Agustí & Antón, 2002; Böhme, 2003).

However, along the Early Miocene, the first signs of change started to emerge. After a slight cooling period, the average global temperatures started to rise in the late Early-Miocene (Zachos et al., 2001). In the Middle Miocene the peak of mean annual temperatures reached 17 - 22 °C, thus referred to as Mid-Miocene Climatic Optimum (MMCO) (Janis, 1993; Zachos et al., 2001). Studies based on stable isotope records have estimated the MMCO in Europe around 14,5 Ma, however peaked globally in slightly different times in each continent (Blois & Hadly, 2009; Böhme, 2003). The increase of average global temperatures has been connected to increase in seasonality which reduced the amount of precipitation throughout Eurasia (Eronen et al., 2010; Fortelius et al., 2002).

Nevertheless, the late Middle-Miocene was also a time of complete turnover in temperatures that is well recognized in stable-isotope record (Agustí & Antón, 2002). Numerous sources show a continuous decrease in temperature following MMCO to end of the Late Miocene (Cerling, Wang, & Quadet, 1993; Eronen & Rössner, 2007; Ivanov et al., 2010; Semprebon et al., 2004). As a result, Bruch et al. (2007) estimated the mean annual temperature to decrease of 7 °C until the end of the Late Miocene. Studies have found that the Late Miocene cooling culminated to decrease of ocean temperatures into similar found today, with

transitions of Northern Hemisphere glaciations and deeper polar temperature gradient (Agustí & Antón, 2002; Herbert et al., 2016).

Increased pole-equator gradient has been indicated to have weakened the evaporative capabilities of atmospheric circulation resulting in decreased precipitation in European latitudes, contributing to pronounced changes in the biota of these regions (Herbert et al., 2016). Thus, Central Europe persisted with generally humid conditions throughout the Middle Miocene, but in southern regions east-west gradient in annual precipitation emerged, with east Europe being drier (Eronen et al., 2010; Fortelius et al., 2002). Additionally, ecomorphological proxies related to the Middle Miocene, show slightly higher aridity in Western-Asia than in Europe (Fortelius et al., 2002). Noteworthy, Mediterranean regions experienced strongest aridity conditions from the Middle to the Late Miocene (Saarinen, Mantzouka, & Sakala, 2020). Nevertheless, at the end of the Late Miocene, the increased aridity was clearly visible in entire Europe and Western Asia (Eronen et al., 2010; Fortelius et al., 2002). Eronen et al. (2010) reconstructed precipitation for central Europe 700 - 1200 mm per year at that time indicating increased aridity, with significant seasonality.

The significant shifts in temperature and precipitation are considered to correspond to global changes in ocean currents, the major uplifts of mountain ranges and continental movements (Fortelius et al., 2002; Janis, 1993). One of the most significant was the collision of the Afro-Arab (isolated since the Late Eocene) and Eurasian plates, that closed the ancient connection between the Atlantic and the Indian Ocean, leading to the closure of the Tethys Sea (Ivanov et al., 2010; Janis, 1993). However, this was just one of many plate - and oceanographic reorganizations along the Miocene epoch (Ivanov et al., 2010). Thus, changes in tectonic activities, sea level fluctuations, opening and closure of marine corridors, and instability of climate had a large-scale impact on both marine and terrestrial ecosystems (Ivanov et al., 2010). Especially, studies have highlighted the establishment of North Atlantic Current that increased heat transportation in south-north axis (Herbert et al., 2016; Janis, 1993). Together with simultaneous opening of Drake's Passage between Antarctica and South America increased cold oceanic circulation, resulting in deeper thermal gradient of surface waters in both poles (Janis, 1993).

In addition, the uplift of Rocky Mountains, Himalayas and Andes along the Miocene forced by plate tectonics, redirected thermal gradients and wind patterns that polarised the global precipitation patterns (Janis, 1993). Furthermore, terrestrial realms experienced faunal turnover as low sea levels contributed land bridges that allowed extensive faunal exchange for the first time from Africa to Europe and respectively from Eurasia to Northern America (Janis, 1993).

Instead, Herbert et al. (2016) suggested that decline in atmospheric CO_2 conducted global forcing mechanism that was major influencer in changes of temperature, seasonality and aridity, and thus

vegetation. Nevertheless, studies show that the flush tropical and sub-tropical vegetation that once covered the central Europe during the Early Miocene, disappeared gradually with changing climate (Eronen et al., 2010; Janis, 1993; Jechorek & Kovar-Eder, 2004). Paleovegetation reconstruction has indicated broad-leaf evergreen forests in westwards regions of modern Austria and respectively temperate broad-leaf deciduous forest in eastwards regions (Jechorek & Kovar-Eder, 2004). These characteristics included oak-dominated cupuliferous species and laraceous species such as laurel, cinnamon and camphor trees (Agustí et al., 2003). In Mediterranean due the lower precipitation throughout the Miocene epoch, the vegetation is estimated to be dominated by thorn shrubs (Janis, 1993).

Consequently, the most prominent effect was the change in the Miocene landscapes, characterized by the development from C_3-dominated closed forests, into more open woodlands and grass vegetation dominated temperate savanna-mosaics (Janis, 1993; Strömberg, Werdelin, Friis, & Saraç, 2007). The shift in environment patterns at the end of the Miocene, is considered to be tied to global cooling and increased seasonality (Herbert et al., 2016; Saarinen et al., 2020). Recent studies have noted that C_4-plants (that is, plants using the C_4 photosynthetic pathway) are better suited for dry and warm conditions with lower atmospheric CO_2 (Cerling et al., 1993; Herbert et al., 2016). These changes that transformed the landscapes in just 8 million years, have been found to have a significant effect on grazing mammals that manifested diverse morphological and ecological changes (Cerling et al., 1993; Janis, 1993). Particularly herbivorous mammalian linages from all continents experienced evolutionary changes, with browsers of forest vegetation being partly replaced by grazers in many parts of the world (Blois & Hadly, 2009). The more abrasive foods created a selective pressure to increase the tooth wear functional durability that established the lineages of modern mixed-feeding and grazing ungulates and their diet diversity (Janis, 2008).

4 ORDER PROBOSCIDEA – ELEPHANTS AND THEIR RELATIVES

Proboscidea is an order of mammals that includes extant elephants and their extinct relatives (Göhlich, 1999). During the Neogene period (23 -2 Ma) proboscideans were a diverse group with hundreds of species (Shoshani & Tassy, 2005) which exhibited a wide range of habitats and climate conditions (Göhlich, 1999). Proboscideans during the Miocene epoch were represented by several sympatric genera which each were distantly related (Göhlich, 1999; Shoshani & Tassy, 2005), see Section 6.1 for species relevant to this study. Proboscideans are mainly known from fossilised remains, thus resulting in debates of taxonomy and classification (Göhlich, 1999; Shoshani & Tassy, 2005). Proboscideans diversity gradually fell after the Middle Miocene high species diversity, yet remaining a much more diverse group than today, until the end of Pleistocene (c. 10 000 Ma). Lastly, the woolly mammoth *(Mammuthus primigenius)* faced extinction of c.

4000 Ma (Shoshani & Tassy, 1996). Today only three species remain; the African forest elephant (*Loxodonta cyclotis*), African bush elephant (*Loxodonta africana*) and Asian elephant (*Elephas maximus*) with few subspecies (Shoshani & Tassy, 2005).

Proboscideans were initially considered to belong to the ungulates, as the manus and carpus are constructed of five toes and fingers surrounded by cushion pads (Göhlich, 1999). However, according more recent findings, proboscideans belong to the Paenungulata, an ungulate-like lineage of afrotherians (O'leary, Roberts, Bouare, Sissoko, & Tapanila, 2006). The Miocene proboscideans were characterized by one to two pairs of tusks, positioned to either upper, lower (see *Deinotherium* in Figure 2) or both jaws (see *Gomphotherium*, respectively), short or long trunk and large size (Göhlich, 1999). Notably, in the Miocene the shoulder height of the largest species reached four meters, thus they were one of the largest land vertebrates ever known (Göhlich, 1999), together with the Oligocene rhino-related indricotheres (Saarinen, 2019).

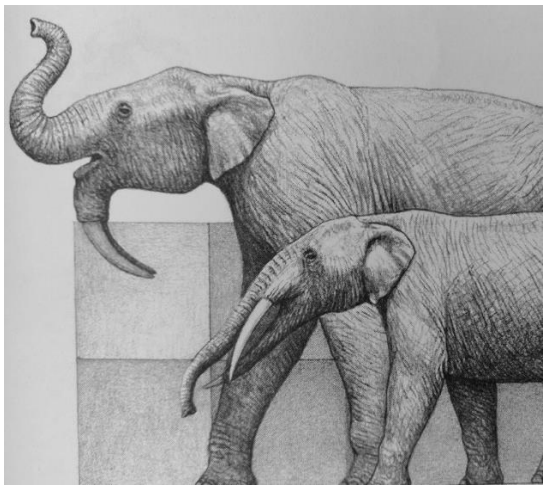


Figure 2. Comparison of the Deinotherium giganteum with pair of lower tusks (back) and Gomphotherium angustidens with lower and upper tusks (front). Size and proportions illustrated are based on set of complete limb bones from Cerecinos del Campo, Spain. (Agustí & Antón, 2002)

Proboscideans likely originated in Africa during the Paleocene (65-56 Ma). Primitive species resembled small-sized hippo-like creatures with elongated body and relative short legs, thus hardly recognizable as ancestor of modern elephants (Agustí & Antón, 2002). During their early evolution proboscideans increased in body size and extend of the trunk (Göhlich, 1999). Adaptations in feeding manifested changes in lower and upper indictors i.e. tusks which formed into diverse morphological forms distinguishable in the proboscideans of the Miocene period (Shoshani, 1998), reaching even extreme forms such as shovel like morphology of lower tusks and lower jaw of *Platybelon* (Agustí & Antón, 2002). The lower pair of tusks became reduced later in proboscideans lineage, thus lacking in modern elephants (Göhlich, 1999). The dentition of proboscideans is further discussed in Section 5.1.

Despite the climatic the stability of the Early Miocene, the tectonic forcing had enormous consequences to further evolution of proboscideans (Agustí & Antón, 2002). The formation of land bridges allowed the proboscideans to leave Africa and eventually they did radiate all around the world, expect Antarctica and Australia (Göhlich, 1999). The time of dispersal of proboscideans out of Africa during the Early Miocene is referred to as the Proboscidean Datum Event (Agustí & Antón, 2002). Three groups of proboscideans included in this study (as discussed in Section 6.1) the gomphotheres, mammutids and deinotheres, were also the first ones to reach Europe. The first were the genera *Gomphotherium* (in the family Gomphotheriidae, see Figure 5 in Section 6.1) and *Zygolophodon* belonging to the family Mammutidae (Göhlich, 1999). *Gomphotherium* spread throughout the Eurasia into North America, unlike other groups of Miocene proboscideans, establishing several sympatric species along the way (Agustí & Antón, 2002). Thus, today over dozen species in gomphotheres are considered valid (Wang et al., 2017). Mammutids were less common, but still widely present in Europe. The third proboscidean group to reach Europe were the deinotheres, (*Prodeinotherium* and *Deinotherium*) with staggeringly different morphology of down curved tusk (Agustí & Antón, 2002). Deinotheres did not occur in Northern Asia nor reached the North America (Göhlich, 1999). One group of gomphotheriid proboscideans later gave rise to modern elephants and their iconic relatives, the mammoths (Göhlich, 1999).

Consequently, the changes in the Miocene climate were key for proboscideans high diversity and wide dispersal (Agustí & Antón, 2002). The earliest proboscideans browsing diet sifting into more prevailing grazing has been documented largely in the fossil record, coincided with the appearance of dominant grass vegetation (Shoshani, 1998; Strömberg et al., 2007). The dispersal into entire world, suggest that these species were exposed to diverse range of environments conditions, driving the evolution of proboscideans into large spectrum of morphological differences and thus in ecological strategies, lastly reflected by diet.

5 STUDYING TEETH

Teeth consist of several layers of varying density and hardness (Ungar, 2015). Dental bone, and especially the outermost layer i.e. tooth enamel, are some of the most durable tissues (Lucas et al., 2013; Ungar, 2015), thus remaining in the fossil strata for a long time. The function of teeth is to guide occlusion i.e. chewing, but also to process the consumed food in mastication (Ungar, 2015). Thus, dentition and diet are inseparable and understanding the morphological differences rising from this relationship are crucial for reconstructing the Miocene proboscideans feeding preferences, as discussed next.

5.1 DENTITION OF PROBOSCIDEANS

The dentition of the proboscideans is composed of six sets of teeth. First erupt the deciduous premolars of second, third and fourth (P2,P3, P4) followed by permanent molars of first, second and third lower molar (M1,M2,M3) with progressive increase of size on each set (Mendoza et al., 2002). Proboscideans have lost canines entirely, but also premolars and molars are reduced in numbers in the course of evolution (Göhlich, 1999). Notably, the tusk are incisors that grow throughout the life of the individual. Dental trends in the course of proboscidean evolution include the increase of size, number of transverse ridges and complexity of the teeth (Shoshani, 1998).

As the dentition reduced, it increased in size, which has been considered to indicate changes in the diet demands (Shoshani, 1998). Hence, the size of mandible became too short to accommodate all premolars and molars at the same time (Göhlich, 1999; Shoshani, 1998). As a result, elephantiformes developed a distinctive characteristic, called horizontal displacement. In this process the juvenile teeth erupt during the lifetime horizontally from the back of the jaw, one by one as smaller teeth are replaced with larger successive teeth behind. Meantime, simultaneously moving slowly forward along the jawbones, respectively in horizontal manner (Shoshani, 1998). As the teeth move, the dental surfaces also wear due the use (von Koenigswald, 2018). As the teeth reach the jaw front, they are completely worn down and in chips forced out from the mouth or swallowed (Göhlich, 1999; Shoshani, 1998).

Along the horizontal displacement, the relative size of each tooth increases. Thus, the elephantiformes jaw can accommodate first three teeth (DP2, DP3, DP4) at the same time, which later in the process reduces to only one (M3), see Figure 4. In the only outer group, the deinotheres *Prodeinotherium* and *Deinotherium*, the teeth erupt in vertical fashion, common for example in humans and horses, that allows jaw to accommodate all the teeth at the same time. Thus, the number of proboscideans molars affected the data collection (see Section 6.2) and the process of horizontal displacement affect the measurement practises, as discussed in next Section of 5.2 and in 7.2 respectively.

Proboscideans have multiple different cheek teeth morphologies indicating differences in the diet and ecology of certain family (Göhlich, 1999; Shoshani, 1998). This study covered three different teeth morphologies i.e. cheek teeth patterns; the bunodont, lophodont and zygodont molars (Göhlich, 1999). Details and terminology are shown next in the Figure 3.

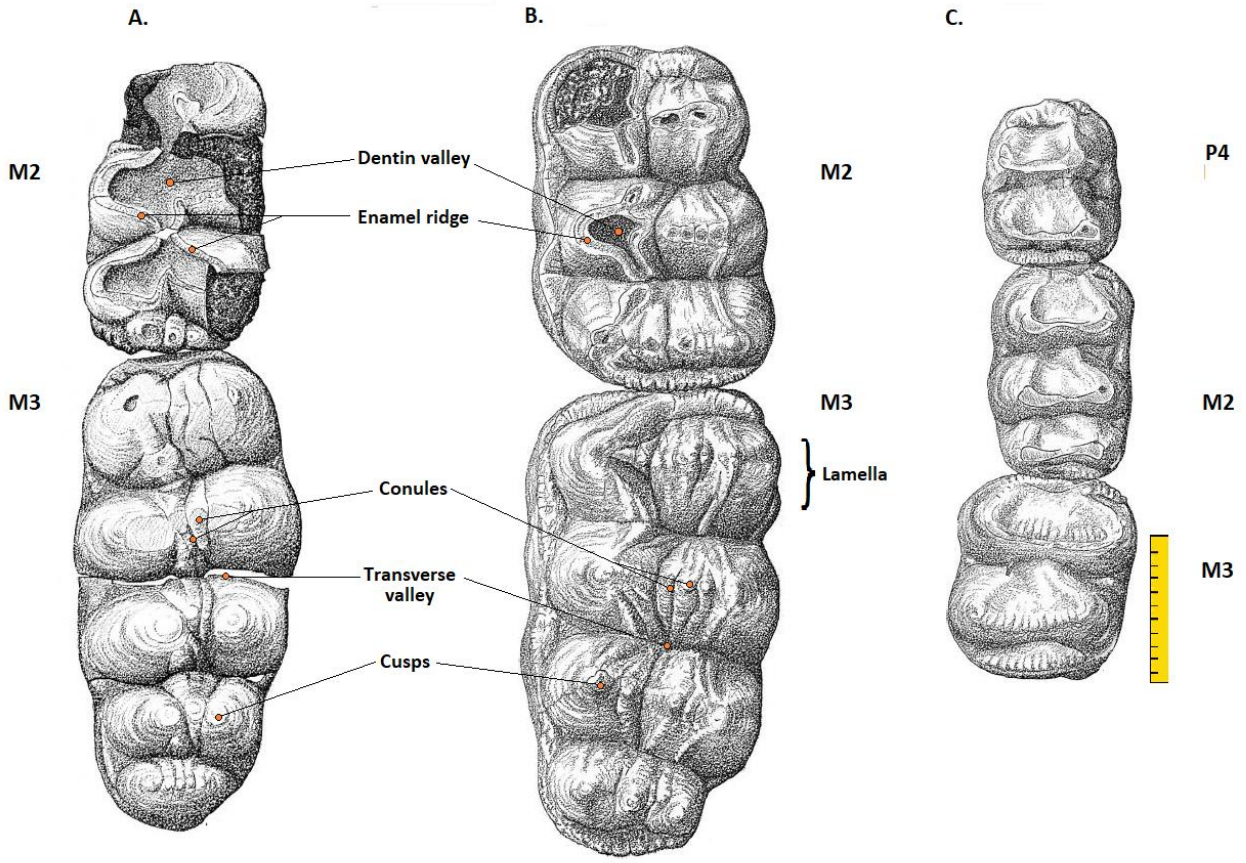


Figure 3. Cheek teeth patterns of proboscideans, yellow scale 5cm. A; Bunodont pattern of gomphotheres. B; Zygodont pattern of mammutids. C; Lophodont pattern of deinotheres. Modified; Göhlich 1999.

The most primitive cheek teeth pattern is the bunodont (Fortelius, 1985; Saarinen, 2019), presented in Figure 3 (A) according Göhlich (1999). Bunodont teeth consist of low-cusped molars (Janis, 2008) and are characteristic for gomphotheres (Göhlich, 1999). Bunodont cusps are round on the top, cone-like and are arranged in pairs (Göhlich, 1999) that are separated by transverse valleys. Between each cusp and also in the transverse valleys, the gap has been partially filled with smaller cusps, defined as conules (Göhlich, 1999). Organized in this fashion next to each other, teeth morphology consists of several transverse ridges, defined as lamella (Göhlich, 1999; Janis, 2008).

In addition to the derived bunodont forms of the gomphotheres, there are bilophodont and zygodont morphology types in the proboscideans (Göhlich, 1999). Firstly, the zygodont cheek teeth pattern (Figure 3, B) is common in mammutids (Göhlich, 1999). Zygodont teeth resembles bunodont teeth, yet the ridges are transferred to sharp crests (Göhlich, 1999) that are integrated together as lophs, connecting the cusp in horizontally (Janis, 2008). Hence, zygodont teeth have higher cusped molars with sharper ridges. Also typical for zygodont teeth are reduced or lacking conules in the transverse valleys (Göhlich, 1999).

Secondly, the bilophodont check teeth pattern (Figure 3, C) is characteristic for deinotheres (Janis, 2008). In lophodont teeth the previously separated cusps combined together into uniform round ridges (Fortelius, 1985), that in bilophodont molar are formed into two transverse cutting ridges. Thus, these low-crowned molars consist of two transverse cutting blades separated by large transverse valleys with additional outer prominent loph on outer (cheek-sided) edge of the tooth (Fortelius, 1985).

5.2 DENTAL WEAR AS INDICATOR OF DIET

Tooth wear results directly from use of the teeth i.e. mastication and occlusion. Tooth wear refers to cumulative removal of dental tissue (Kaiser et al., 2013) that is visible to naked eye on the profile of the molar as a loss of enamel and eventually dentine, for illustration see Figure 4. The change in the shape of the tooth is caused both by the contact between the teeth and by the characteristic wear caused by the plant parts contained in the animal's diet, as will be detailed later in this chapter. The juvenile teeth have intact cusps and enamel surfaces. However, the physical properties of the foods modify gradually the shape and height of the molars, thus reducing the functionality of it. Reduction of cusp profile eventually reveals dentine under the enamel (von Koenigswald, 2018), which is termed as moderate state of wear (Saarinen et al., 2015).

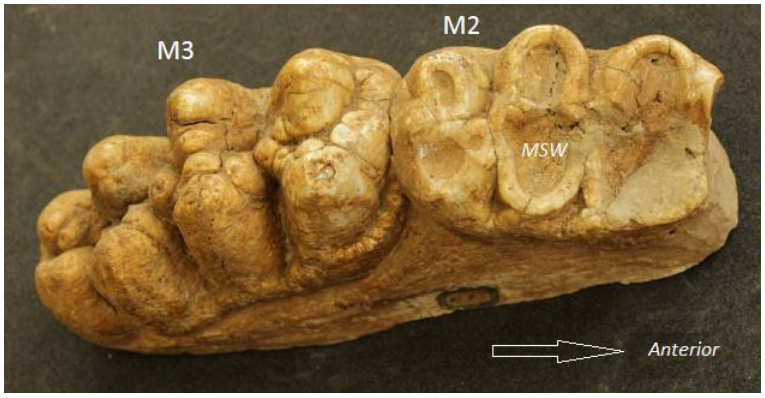


Figure 4. Illustration of dental wear process of bunodont molars remained as attached on jawbone. On the left unworn, recently erupted M3. On the right progressively worn M2, as anterior parts heavily worn (partially broken) and lightly worn posterior parts. MSW stands for moderate stage of wear. Arrow shows the direction of horizontal displacement i.e. tooth eruption direction.

In addition, the process of wear differentiates according the cheek teeth pattern. In lophodont teeth, dental wear forms facets i.e. smooth and even surfaces on the enamel, that creates sharp cusps (von Koenigswald, 2018). Instead, in the bunodont and zygodont teeth the occlusal surface flattens and forms a dentin valley that is surrounded by thin enamel ridge as softer dentine erodes faster than relatively harder enamel (Göhlich, 1999; von Koenigswald, 2018). Eventually in very last wear stages only dentine stump is left that has lost it functional ability (von Koenigswald, 2018). However, due the horizontal displacement, the teeth worn unevenly in anterior-posterior direction as firstly erupted lamellae face higher rate of wear

than later erupted posterior lamellae (Sanders, 2018). The lamellae that are in moderate stage of wear are an essential indicator of the effect of diet and thus the basis of the research method (Saarinen et al., 2015), as shown in Section 7.1.

Tooth wear is caused by two sperate processes; the attrition (tooth-to-tooth contact) and abrasion (tooth-to-food contact), however acting simultaneously on the occlusal surfaces i.e. working surfaces of the molars (Fortelius, 1985;). Attrition becomes dominant when primary cause of wear are the teeth working against each other through soft plant material such as dicotyledonous plants (Ackermans, 2020). Abrasion instead dominates when the diet composes highly abrasive items and/or mineral particles (Kaiser & Fortelius, 2003). In grass-utilizing herbivores it has been considered that the food itself contributes more to dental wear than teeth contacting each other, which tends to obscure facets, thus results in dulling the cusps (Green & Croft, 2018). Instead, the attrition creates sharp enamel surfaces that are generally displayed in browsers (Fraser & Theodor, 2011).

The most significant cause of abrasion in dental wear is still unclear, but according to current knowledge, the teeth of herbivores are abraded by large amounts of (internal) hard (opaline) silica compounds and fibrous particles contained in the grass that are considered highly abrasive (Ackermans, 2020; Damuth & Janis, 2011; Fortelius, 1985; Janis, 2008; Janis & Fortelius, 1988; Saarinen, 2019). Furthermore, grass is considered nutrient poor, thus necessitating higher food intake and repeated chewing that results heavy wear on the enamel (Janis, 1988). Other studies have further suggested the role of external grid and dust accumulated on the surfaces of the plant food to increase tooth wear, that is generally due the observations of correlation between grazing and open - and dry environments (Janis, 1988; Janis & Fortelius 1988; Ungar, 2015).

The wear has significant role on the survival of the individual as the over worn teeth hampers the acquisition and processing the food, resulting not only lower food intake but also lower nutritive value of it (Lucas *et al.*, 2013; Ungar, 2015). This often forces to compensate either by eating more or chewing longer (Janis and Fortelius, 1988; Ungar, 2015). Eventually consequences will even be decreased of fitness and reproductive viability (Ungar, 2015). After all, tooth wear determines an individual's survival.

6 MATERIALS

The materials of this study were fossilised molars of study genera introduced below. The materials were not available in Finland, thus I visited in Natural History Museum of Vienna. Furthermore, the materials

were supplemented with unpublished data. In the Miocene timescale, in total of 32 localities were found as discussed lastly in this Section.

6.1 STUDY GENERA

Proboscideans relevant for this study can be divided into groups based on cheek teeth morphology, illustrated in Figure 5. In this study the subjects of research are following genera of proboscideans; *Choerolophodon, Deinotherium, Gomphotherium, Konobelodon, Prodeinotherium, Tetralophodon* and *Zygolophodon* (Göhlich, 1999). These study genera were chosen according to their presence in the Miocene Europe from available specimens.

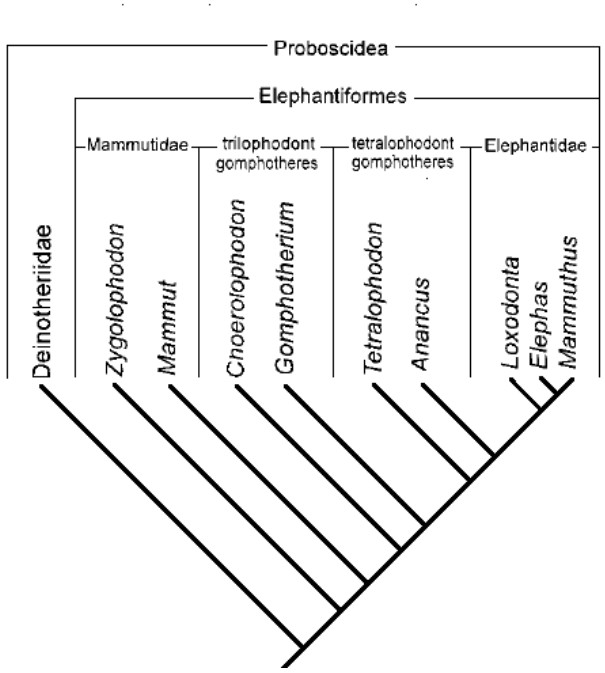


Figure 5. Simplified classification of the Proboscidea in Eurasia during the Miocene epoch (modified after Shoshani & Tassy, 1996*, based in a cladogram).*

Under suborder Elephantiformes, family Mammutidae is characterized by zygodont teeth, found in *Zygolophodon*. Gomphotheres comprise species with bunodont cheek teeth patterns. Further, based on the number of lops in intermediate molar (M2) the family Gomphotheriidae are divided into two morphological groups: the primitive group of "trilophodont gomphotheres" (3 lamellae) including *Choerolophodon* and *Gomphotherium,* and the more derived "tetralophodont gomphotheres" (4 lamellae) including the derived amebelodontine *Konobelodon* and the tetralophodontine *Tetralophodon*. The tetralophodontine gomphotheres also include the lineage that gave rise to the true elephants (Elephantidae) which eventually evolved lamellar, hypsodont dentition, including the derived lineages of modern elephants (*Loxodonta* and *Elephas*) and their extinct relatives, the mammoths (*Mammuthus*). On the other hand, family

Deinotheriidae is a conservative group with most outstanding dental characteristics with bilophodont teeth. These include the conservative *Prodeinotherium* and more derived, latter *Deinotherium.* They are considered to be the sister group of Elephantiformes. (Göhlich, 1999)

6.2 DATA COLLECTION

The material for this study was fossilised molar teeth of proboscideans from the Miocene. These molar specimens comprised lophodont, bunodont and zygodont cheek teeth patterns. The majority of specimens consisted of individual molars, while a small proportion were still attached to mandibula or maxilla. The material was acquired from Natural History Museum of Vienna (Naturhistorisches Museum Wien) and supplemented with data housed in Natural History Museum of London (Unpublished data, 2020). The localities environment data was collected NOW - the New and Old Worlds database (NOW, 2020) and vegetation pattern data from available literature (Strömberg et al., 2007; Utescher et al., 2017).

I selected the molars based on macroscopic tooth wear rate on the profile of the molars and sample availability. According to Saarinen et al. (2015), I included all adult molars representing a moderate stage of wear, see clarification in Section 5.2. For the measurements, when multiple molars were attached to jawbone, the order of preference was third (M3), second (M2) and first molar (M1). Dentition from upper and lower jaws were taken into account as studies have not indicated significant difference in mesowear angles between them (Kaiser & Fortelius, 2003; Saarinen et al., 2015). Juvenile molars were excluded according to DeMiguel et al. (2001) in order to have homogeneity in the populations. Furthermore, I excluded from the measurements the separated fragments of teeth cusps or molars with too badly preserved enamel surfaces e.g. over worn lamellae.

The fossil specimens were labelled with information of timing, species, locality and molar identification. However, most of the information dated to 19th century and the begin of 20th century. Thus, specimen information required updating as species taxonomy and geologic time scaling have refined since.

6.3 GEOGRAPHICAL LOCALITIES AND TIMESCALE

This study discusses of Miocene epoch expanding ca. 23 - 5 Ma (Cohen et al., 2013). I concentrated on the Miocene time period, because of its significance in the proboscidean's evolution due rapid changes in climate and environment regimes at that time. Age of each locality were gathered from NOW database (NOW, 2020). Consequently, the time span of this study covers the European Land Mammal Zones (MN) from MN 5 to MN 13.

The molar specimens belong fossil sites in six countries as follows; Austria, France, Germany, Iran, Pakistan, and Spain. In total the data consisted of 32 localities. Localities were combined according the country and timing, is cases which the sample size was lower than three on individual locality, to clarify the results and for improved statistical significance. Thus, the data analysed gives comprehensive window to entire Eurasian proboscidean biota during the Miocene (Göhlich, 1999). A map of the localities included in this study is shown in Figure 6.

Figure 6. Study localities in Europe and Western-Asia.

1. *Burgos*
2. *Dera Bugti*
3. *Eibestal bei Mistelbach*
4. *Eibiswald*
5. *Eichkogel*
6. *Eppelsheim*
7. *Inzersdorf*
8. *Josefsberg*
9. *Kettlasbrunn*
10. *Kohfidisch*
11. *Laaerberg*
12. *Leithagebirge*
13. *Mannersdorf*
14. *Maragheh*
15. *Meidling*
16. *Mistelbach*
17. *Paasdorf*
18. *Pontlevoy-Thenay*
19. *Reichertshausen*
20. *Sacedon*
21. *Sansan*
22. *Simorre*
23. *St. Gaudens*
24. *Stratzing*
25. *Türkenschanze*
26. *Wien*
27. *Wien-Belvedere*
28. *Wienerbecken*
29. *Wilfersdorf*
30. *Villaluenga*
31. *Villaobispo*
32. *Villefranche d'Astarac*

7 METHODS

I used mesowear angle method introduced by Saarinen et al. (2015) to characterize the diets of proboscideans from Miocene period. In this study, the diet is referred as common generalization of ungulates' feeding ecologies of browser, mixed feeder and grazer. I applied the method on molar teeth of the proboscidean species included in this study, representing moderate state of wear. I measured

mesowear angles from dentine valleys and facets preserved on fossilised occlusal surfaces. These were further analysed with statistical analyses of Wilcoxon signed-rank test and linear regression established on data-based calculations, as discussed in Section 7.2.

7.1 MESOWEAR ANGLE METHOD AS A PROXY OF DIET

Mesowear methods comprise a group of tooth wear techniques commonly used in paleoecological studies for dietary interpretation in extinct ungulates (Ackermans, 2020; Fortelius & Solounias, 2000; Rivals, 2012). As discussed in the introduction, mesowear comes from a standpoint between dietary signal of microwear (the few last days of individuals lifetime) and slow evolutionary changes of morphology of the entire tooth (Fraser & Theodor, 2011; Mendoza & Palmqvist, 2008). Thus, mesowear indicates diet over the span of months and years of individual's life (Fortelius & Solounias, 2000).

Mesowear methods measure the dietary attrition and abrasion resulting from physical properties of foods, that induces wear of enamel on occlusal surfaces of the ungulates' molars (Fortelius & Solounias, 2000; Fraser & Theodor, 2011). The original mesowear method (mesowear I), introduced by Fortelius & Solounias (2000), records dental wear by scoring the height and sharpness of molar cusps of selenodont and trilophodont cheek teeth patterns common in e.g. ruminants. In this study I used mesowear angle method introduced by Saarinen et al. (2015) which is extension of mesowear I – method which according to Saarinen et al. (2015) cannot be used for proboscideans as such due differences in chewing technique and oblique rubbing of occlusal surfaces. The mesowear angle method is a relatively new technique so far applied for proboscideans and xenarthrans such as sloths and armadillos (Saarinen & Karme, 2017; Saarinen et al., 2015).

Mesowear angle method evaluates worn molar surfaces as proxies for feeding ecology (Saarinen et al., 2015; Saarinen & Karme, 2017; Green & Croft, 2018). Mesowear angles reflect the height of the occlusal relief, i.e. the height of enamel ridges relative to the bottom of dentine valleys representing moderate state of wear. The distance between the bottom of dentine valley and the top of the enamel ridge correlates with the measured geometrical angle.

Recording of the occlusal relief reflects the previously discussed relative attrition vs. abrasion domination in feeding. Abrasive plant material (especially grass) induces higher wear rate on the hard enamel tissue at the occlusal surfaces of the molars (Saarinen et al., 2015). Highly abrasive material wears the enamel and dentin equally, thus resulting in flatter occlusal relief reflected in larger angles (Saarinen et al., 2015) Contrarily, softer plant material enables higher tooth-to-tooth contact that accelerates the wear of softer dentin over the harder enamel (Saarinen et al., 2015). Thus, it results in carving effect with deeper valleys

that maintains higher occlusal relief reflected in narrow angels (Saarinen et al., 2015). Thus, mesowear angle indicates average diet signal of individuals and populations providing robust interpretations of feeding ecology (Green & Croft, 2018).

The attrition-abrasion gradient is used for determining grazers from browsers based on height of the occlusal relief (mesowear angles), and thus the amount of abrasion experienced by the teeth while feeding (Saarinen & Lister, 2016). By measuring dental wear as mesowear angles, it is thus possible to generate predictions about proboscideans diets from Miocene epoch. In this study mean mesowear angles are considered to indicate pure browsing (<10% grass in the diet) as the mean mesowear angle is relatively sharp showing angle of <106 ˚ and respectively indicate grazing diet (>90 % grass in the diet) as mean mesowear angle is >130 ˚ according Saarinen et al. (2015), see Figure 7. In between are the intermediate angles of mixed-feeding of 106 - 130 ˚, which are further divided into 106 - 113 ˚ indicating browse-dominated mixed-feeding and 124 - 130 ˚ indicating grass-dominant in mixed-feeding.

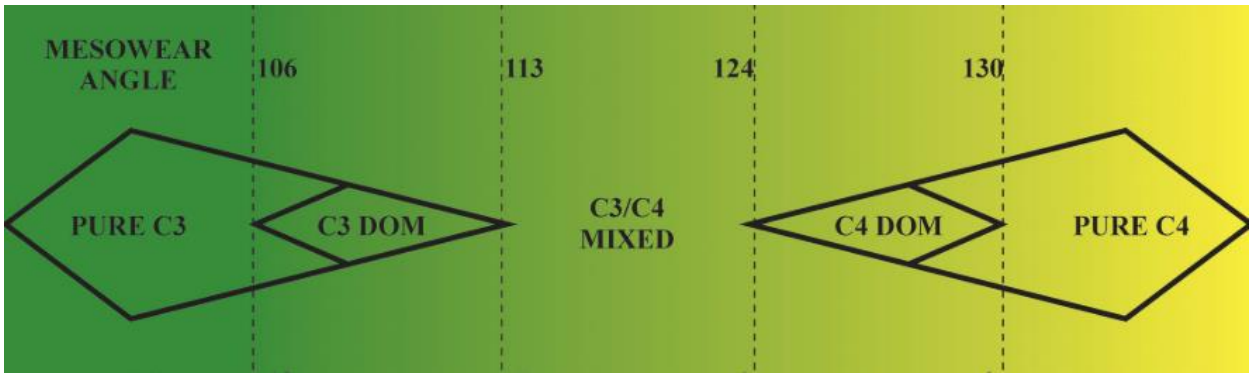


Figure 7. The dietary spectrum of proboscideans from tropical Africa and Asia with mean mesowear angles and corresponding feeding preferences. 106 ˚ corresponding to pure C_3-diet i.e. browsing. 106 - 113 ˚ corresponding to browse (C_3)-dominated mixed-feeding. 106 - 130 ˚ corresponding to general mixed- feeding and 124 - 130 ˚ of grass (C_4)-dominant mixed-feeding. Over 130 ˚ corresponding to pure grazing.

7.2 MEASUREMENT TECHNIQUE

I measured the mesowear angles with an electronical angle meter, that has been modified as explained in Saarinen et. al (2015) for this method, see Figure 8A. The two arms of the device provide the geometrical angle according the openness of the arms, see Figure 8B. Also, to proximal ends of both arms has been added extendable small metal plates that meet on the tip, that enables measurement precision of 0,1˚ (Saarinen et al., 2015).

Measurements were taken from occlusal surfaces of molars on each lamella representing moderate state of wear (Saarinen et al., 2015). Firstly, bunodont and zygodont teeth patterns were measured as mesowear angles. The measurements were taken as follows; I placed the vertex on the deepest part of the dentine valley and extended the arms as tangents to the top of enamel ridges surrounding the dentine valley

according the Saarinen et al. (2015), for illustration see 8C. Thus, the measured angles recorded the wear of dental enamel, hence indicating the abrasiveness of the diet (Saarinen et al., 2015; Saarinen & Karme, 2017).

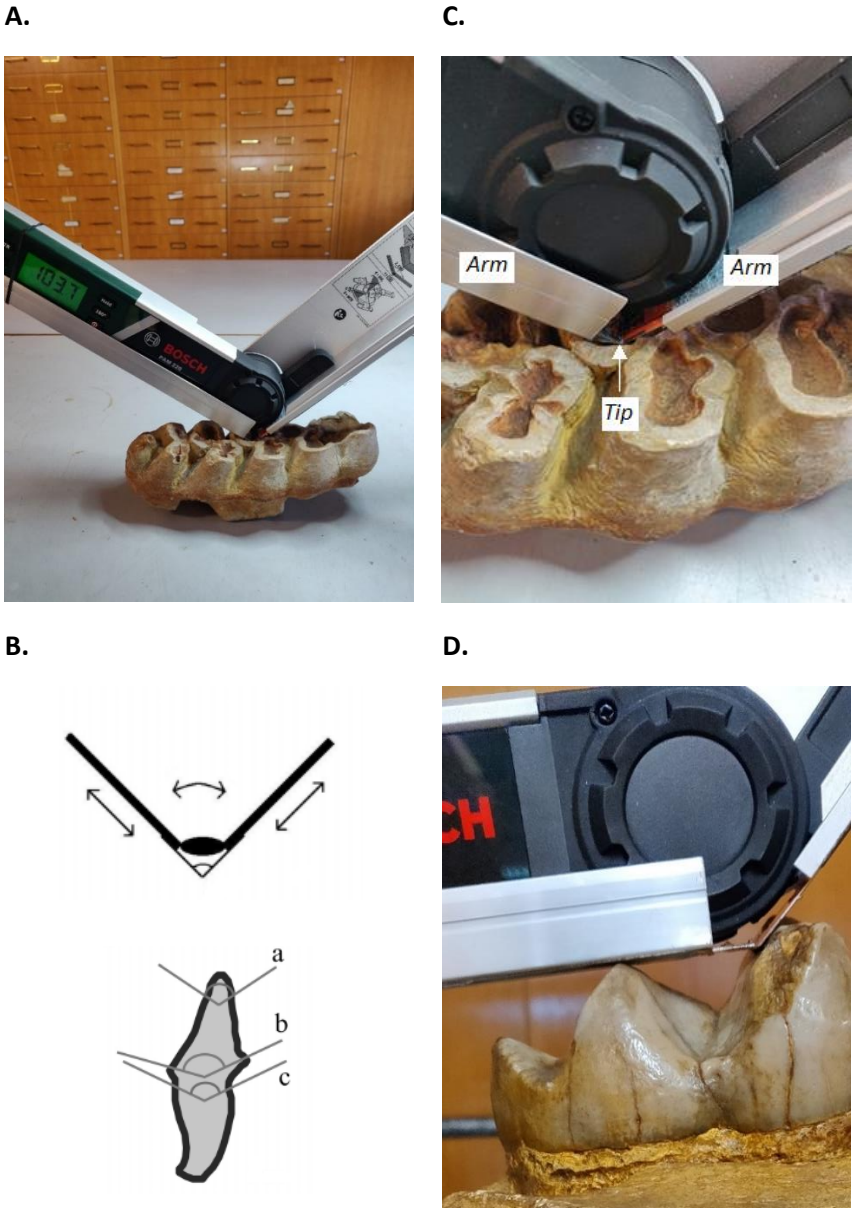


Figure 8. A: Electronical angle meter. B: Extension of the device and illustration of angle differences depending on the width of the dentine valley. In this study used the angle b, the widest part. C: Measurement technique from dentine valley. D: Measurement technique of facet.

Secondly, lophodont tooth wear patterns were measured as facet angles, because easily measurable dentine valleys were absent, as discussed in Section 5.2. Facet angles were measured from each lamella showing facet formation i.e. smooth and flat area on the occlusal surface of a molar (von Koenigswald, 2018). I set the first arm along the direction of the facet and respectively the second arm along the

direction of occlusal surface, for illustration see Figure 8D. However, molars with visible facet formation, but in absence of dentine valleys, were measured accordingly as facet angles, that is in bunodont and zygodont teeth patterns. The facet angles were converted to mesowear angles with following calculations according Saarinen et al. (2015), as illustrated in Figure 9.

$$C = 180° - A$$

$$B = 180° - 2 \times C$$

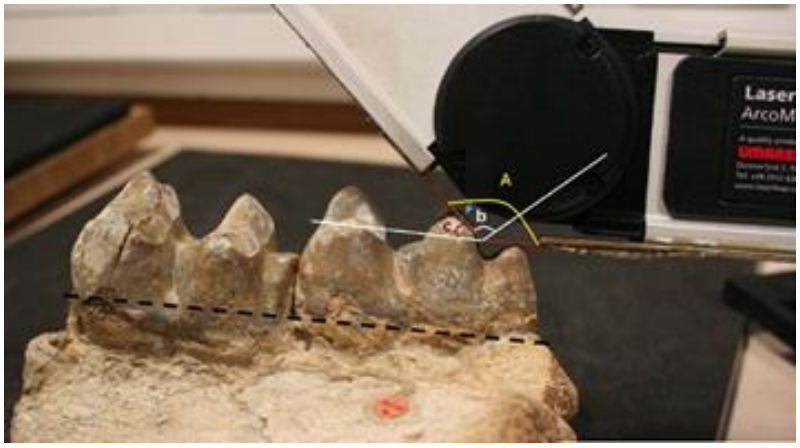


Figure 9. Conversion of the facet angles into mesowear angles. Dashed line shows the general direction of occlusal surfaces.

7.3 CALCULATIONS AND STATISTICAL ANALYSES

I calculated mean mesowear angle for each molar specimen as arithmetic mean of all measured lamellae. Further, I calculated the average mean mesowear for each paleopopulation that allowed to determine the significant differences between the feeding preferences. Taking the locality mean mesowear angle of all paleopopulations present in each locality, constituting paleocommunities, allowed me to explore the interactions of the sympatric proboscideans and their relationship with the environment characteristics and vegetation patterns.

7.3.1 Mean mesowear angle of each specimen

Following the measuring the mesowear angles from all lamellae representing a moderate state of wear, I calculated the mean mesowear angle for each molar in order to provide comparable measurements. The data showed large variation on the number of lamellae under moderate stage of wear, variating between 1-6 with average of 2 resulting from anterior dominant wear process (see Section 5.2). Thus, I calculated arithmetic mean of all measured lamellae in each molar specimen.

7.3.2 Average mean mesowear angle of each proboscidean paleopopulation

Likewise, based on mean mesowear angle of each molar, I further calculated the average mean of each proboscidean species found in same locality-specific deposit, thus, discussed as paleopopulation found on certain locality. For example, the *Choerolophodon pentelici* found in the locality of Maragheh represents one paleopopulation, see Table 1. In some cases, the data of a species from a locality constituted a single specimen. These single datapoints were combined based on two following parameters; on the age of the deposit obtained from NOW-database (NOW, 2020) and with the geographical range of modern countries or sedimentary basins, in order to provide reasonable analysis with increased statistical significance. If not possible, these data points were removed from the analysis.

7.3.2.1 Wilcoxon signed-rank test

Mean mesowear angle of each proboscidean palaeopopulation, were compared using Wilcoxon signed-rank test. Wilcoxon signed-rank test is a non-parametric statistical test that compares each paleopopulation pairwise, to assess whether differences in the means of each pair are statistically significant. The Wilcoxon signed-rank test is optimal for data that cannot be assumed to be normally distributed. Thus, Wilcoxon is the non-parametric equivalent to Student's t-test. Data analysis was performed using JMP Pro 14 (2020). I fitted the mean mesowear angle of each palaeopopulation as response variable Y, against the each palaeopopulation as factor X. These fitted pairs were then analysed using Wilcoxon analysis. This allowed me to evaluate whether there are statistically significant differences in the dietary preferences of proboscidean palaeopopulations. (Rosner, Glynn, & Lee, 2006)

7.3.3 Mean mesowear angles of paleocommunities

The data showed seven localities constituting more than one proboscidean taxa, indicating the presence of community structure of the proboscideans with temporal and spatial variation. Hence, each locality with more than one sympatric proboscidean taxon is referred to as a paleocommunity. These constitute the localities or composite-localities of Eibiswald, Eppelsheim, Maragheh, Pannonian Basin (MN9-10), Sansan and Villefranche d'Astarac, for details see Table 2. As each paleocommunity comprises several species with each their own average mean mesowear signal, for the further analysis, I calculated the arithmetic mean from the population level means termed as locality mean mesowear of each paleocommunity.

Firstly, in order to evaluate the relationship of measured mesowear angles and environment conditions, the mesowear angles of found proboscidean paleocommunities were compared against the locality mean hypsodonty value (collected from the NOW-database). In paleoecological reconstructions, the past herbivorous communities provide opportunity to explore the relationship of diet and vegetation patterns in

the past habitats. Additionally, previous studies have shown that mean hypsodonty values of large herbivorous mammal communities correlate with several environment parameters such as habitat openness, precipitation and amount of external grit in the diet resulting from dry and open environments (Eronen et al., 2010; Fortelius et al., 2002; Janis, 1995; Janis & Fortelius, 1988; Kaiser et al., 2013; Mendoza et al., 2002).

Thus, I compared the locality mean mesowear angles of the paleocommunities to the locality specific mean hypsodonty values, to evaluate whether the obtained mesowear angles correlate with the environment factors such the general openness and aridity of the environment. For the Pannonian basin, that constitutes several localities (i.e., Austrian localities of Inzersdorf, Laaerberg, Mistelbach, Meidling, Stratzing, Wien-Belvedere and Wien 3), I calculated the arithmetic mean from the locality specific hypsodonty values. To examine this, I used linear regression of standard least squares in JMP Pro 14 (2020).

Secondly, to understand the correlation between the diet and the vegetation patterns of the Miocene epoch, recent paleobotanical literature was compared against the dietary signals of proboscideans, due to the lack of sufficient direct environmental data such as records of grasses pollen distributions, as further discussed in Section 9.4. For the analysis the following recent paleobotanical studies were chosen: Utescher et al. (2017), which presents the Late Miocene vegetation reconstructions of the Pannonian Basin based on plant fossil data, and Strömberg et al. (2007) that reconstructs the vegetation structure in Greece, Turkey and Iran (the locality of Maragheh) during the Miocene epoch based on soil phytolith samples.

8 RESULTS

The distribution of mean mesowear angles of proboscideans, combined into paleopopulations, are presented in Figure 10. The average mean mesowear angles are given in Table 1, that provides an overview of the details of each paleopopulations with sample sizes. Dietary interpretations shown in Table 1 were inferred from average mean mesowear angles, according to Saarinen et al. (2015) and Saarinen &Lister (2016). Statistically significant differences between proboscidean paleopopulations based on Wilcoxon signed-rank test are presented in Appendix 1. In total of 165 dental specimens were analysed, shown in Appendix 2.

Table 1. The average mean mesowear angles of the proboscidean paleopopulations with inferred diets.

Family	Paleopopulation	Geographic area	Timing	Age	n	A. mean mesow.	Inferred diet
Deinotheriidae	*Deinotherium giganteum*, Austria (MN7-8)	Central Europe	Middle Miocene	MN 7-MN 8	2	90,5	browser
Deinotheriidae	*Deinotherium giganteum*, Austria (MN9-12)	Central Europe	Late Miocene	MN 9-MN 12	5	84,1	browser
Gomphotheriidae	*Gomphotherium subtapiroideum*, Eibiswald (Austria)	Central Europe	Early Miocene	MN 5	3	114,8	mixed-feeder
Deinotheriidae	*Prodeinotherium bavaricum*, Eibiswald (Austria)	Central Europe	Early Miocene	MN 5	1	87,9	browser
Deinotheriidae	*Deinotherium giganteum*, Kettlasbrunn (Austria)	Central Europe	Middle-Late Mio	MN 7-MN 8	2	104	browser
Deinotheriidae	*Deinotherium giganteum*, Mannersdorf (Austria)	Central Europe	Late Miocene	MN 9-MN 12	3	88,1	browser
Deinotheriidae	*Deinotherium giganteum*, Wienerbecken (Austria)	Central Europe	Late Miocene	MN 9-MN 12	2	94,8	browser
Deinotheriidae	*Deinotherium giganteum*, Wilfersdorf (Austria)	Central Europe	Late Miocene	MN 9-MN 12	3	93,6	browser
Mammutidae	*Zygolophodon turicensis*, St. Gaudens (France)	Western Europe	Middle Miocene	MN 7-MN 8	5	92,4	browser
Gomphotheriidae	*Gomphotherium angustidens*, Sansan (France)	Western Europe	Middle Miocene	MN 6	12	117,2	mixed-feeder
Deinotheriidae	*Prodeinotherium bavaricum*, Sansan (France)	Western Europe	Middle Miocene	MN 6	1	81,2	browser
Gomphotheriidae	*Gomphotherium angustidens*, Simorre (France)	Western Europe	Middle Miocene	MN 7-MN 8	4	97,7	browser
Deinotheriidae	*Prodeinotherium bavaricum*, Pontlevoy-Thenay (France)	Western Europe	Early Miocene	MN 5	2	92,7	browser
Gomphotheriidae	*Gomphotherium angustidens*, Villefranche d'Astarac (France)	Western Europe	Middle Miocene	MN 7-MN 8	4	116	mixed-feeder
Deinotheriidae	*Prodeinotherium bavaricum*, Villefranche d'Astarac (France)	Western Europe	Middle Miocene	MN 7-MN 8	1	83,3	browser
Mammutidae	*Zygolophodon turicensis*, Villefranche d'Astarac, (France)	Western Europe	Middle Miocene	MN 7-MN 8	2	96,9	browser
Deinotheriidae	*Deinotherium giganteum*, Eppelsheim (Germany)	Central Europe	Late Miocene	MN 9	25	92,7	browser
Gomphotheriidae	*Tetralophodon longirostris*, Eppelsheim (Germany)	Central Europe	Late Miocene	MN 9	29	105,1	browser/browse-dominated
Gomphotheriidae	*Tetralophodon longirostris*, Reichertshausen (Germany)	Central Europe	Miocene	MN 1-MN9	3	110,2	browse-dominated
Gomphotheriidae	*Choerolophodon pentelici*, Maragheh (Iran)	Western Asia	Late Miocene	MN 12	15	124,2	grass-dominated
Gomphotheriidae	*Konobelodon atticus*, Maragheh (Iran)	Western Asia	Late Miocene	MN 12	3	85,7	browser
Deinotheriidae	*Deinotherium giganteum*, Pannonian Basin (MN9-10)	Central Europe	Late Miocene	MN 9-MN 10	8	86,6	browser
Gomphotheriidae	*Tetralophodon longirostris*, Pannonian Basin (MN9-10)	Central Europe	Late Miocene	MN 9-MN 10	11	106,4	browser/browse-dominated
Gomphotheriidae	*Gomphotherium angustidens*, Pannonian Basin (Miocene)	Central Europe	Miocene	Miocene	3	113,8	mixed-feeder
Gomphotheriidae	*Gomphotherium cooperi*, Dera Bugti (Pakistan)	Southern Asia	Early Miocene	MN 4	8	104,5	browser
Gomphotheriidae	*Gomphotherium angustidens*, Spain (MN4)	Western Europe	Early Miocene	MN 4	6	111,7	browse-dominated

8.1 Diets of Miocene proboscideans

All paleopopulations of *Deinotherium giganteum* in Austrian localities (Austria MN 7 – MN 8, Austria MN 9 – MN 12, Kettlasbrunn, Mannersdorf, Wienerbecken and Wilfersdorf) show on average sharp mesowear angles, varying between ca. 84 - 104 ˚, indicating pure browsing diet. The considerable variation in mesowear angles within *Deinotherium giganteum* populations of most of the localities, is likely due the small sample size. Solely, the population from Kettlasbrunn shows less variation. Likewise, the *Deinotherium giganteum* population in Eppelsheim (Germany) shows on average browse-based dietary signal of ca. 93 ˚, with considerable variation in mean mesowear angles between ca. 74 - 114 ˚, suggesting perhaps higher variation in the browse-based diet, or higher variation in wear stages due to larger sample size.

The difference of mean mesowear angles between *Deinotherium* and *Gomphotherium* is clear (see Figure 10). In the *Gomphotherium* from the Early Miocene (MN 4), the average mean mesowear angles suggest pure browsing or browse-dominated mixed-feeding, that during the Middle Miocene (MN 6 – MN 8) implies shift on feeding preferences to more generalized mixed-feeding, as shown in Table 1. *G. cooperi* from the Early Miocene (MN 4) shows the sharpest mesowear angles (on average ca. 105 ˚), indicating pure browsing diet. *G. angustidens* from Spain (MN 4), shows on average mean mesowear angle of ca. 112 ˚, indicating browse-dominated mixed-feeding. Two populations of *G. angustidens* from the Middle Miocene France (Sansan and Villefranche d'Astara), show both on average mean mesowear angles between ca. 116 -

117˚, suggesting generalized mixed-feeding during MN 6 – MN 8. Surprisingly, the *G.angustidens* from Simorre (MN 7 – MN 8), shows on average mean mesowear signal of ca. 97˚ indicating on average pure browsing. This interesting variation within species is further discussed in Section 9. Lastly, the G. *angustidens* population from Pannonian Basin constitutes from three samples with discontinuity timing, thus discussed with time span of the Miocene epoch. The Table 1 shows on average mean mesowear angles of ca. 114 ˚, suggesting generalized mixed-feeding for this population, respectively addressed with caution due small sample size and differences in timing.

Prodeinotherium bavaricum has low sample sizes from localities in Austria and France. However, the previous studies have suggested similarity with *Deinotherium*'s feeding preferences (Calandra et al., 2008; Cerling, Harris, & Leakey, 1999). The *P. bavaricum* from Austria shows on average mean mesowear angle of ca. 88 ˚, indicating pure browsing diet. Furthermore, the specimens from France (Sansan and Villefranche d'Astarac) show average mean mesowear angles of ca. 81 ˚ and ca. 83 respectively, indicating similar diet. The population from Pontlevoy-Thenay follows the same trend with on average slightly blunter mean mesowear angle of ca. 93 ˚, suggesting pure browsing diet. Taken together, these results suggest that there is a similar trend in Miocene deinotheres and findings of previous studies (Calandra et al., 2008; Cerling et al., 1999; Saarinen et al., 2015) as further discussed in Section 9.

Surprisingly, *Zygolophodon* was a less common species in the data despite it's wide distribution throughout Europe during the Miocene epoch (Göhlich, 1999). Nevertheless, *Zygolophodon turicensis* from two localities of France (St. Gaudens and Villefranche d'Astarac) shows on average sharp mean mesowear angles of (92 - 97 ˚) thus, indicating pure browsing diet during the Middle Miocene (MN 7 – MN 8).

Notably, *Tetralophodon longirostris* from Eppelsheim (Germany) shows on average mean mesowear signal of 105 ˚ with high variability between ca. 87 - 119 ˚, indicating intermediate dietary signal between pure browsing and browse-dominated mixed-feeding, yet with considerable flexibility in feeding preferences. The population from Reichertshausen shows slightly blunter mean mesowear angle of on average 110 ˚, still consistent with browse-dominated diet for German localities. Lastly, *T. longirostris* from the Pannonian Basin, show on average mean mesowear angles of ca. 106 ˚, which is consistent with observed characteristics of Miocene *Tetralophodon* (Eronen & Rössner, 2007; Saarinen, 2019).

The single most striking observation to emerge from the data comparison was the grazing signal (on average 124˚) of the *Choerolophodon* population from Maragheh, Iran. Instead, *Konobelodon* from Maragheh shows significantly lower mean mesowear angle (ca. 86), indicating pure browsing diet. Hence, these results indicate dietary niche separation of these sympatric species which significance is discussed in more detail in following Sections of 8.2 and 9.

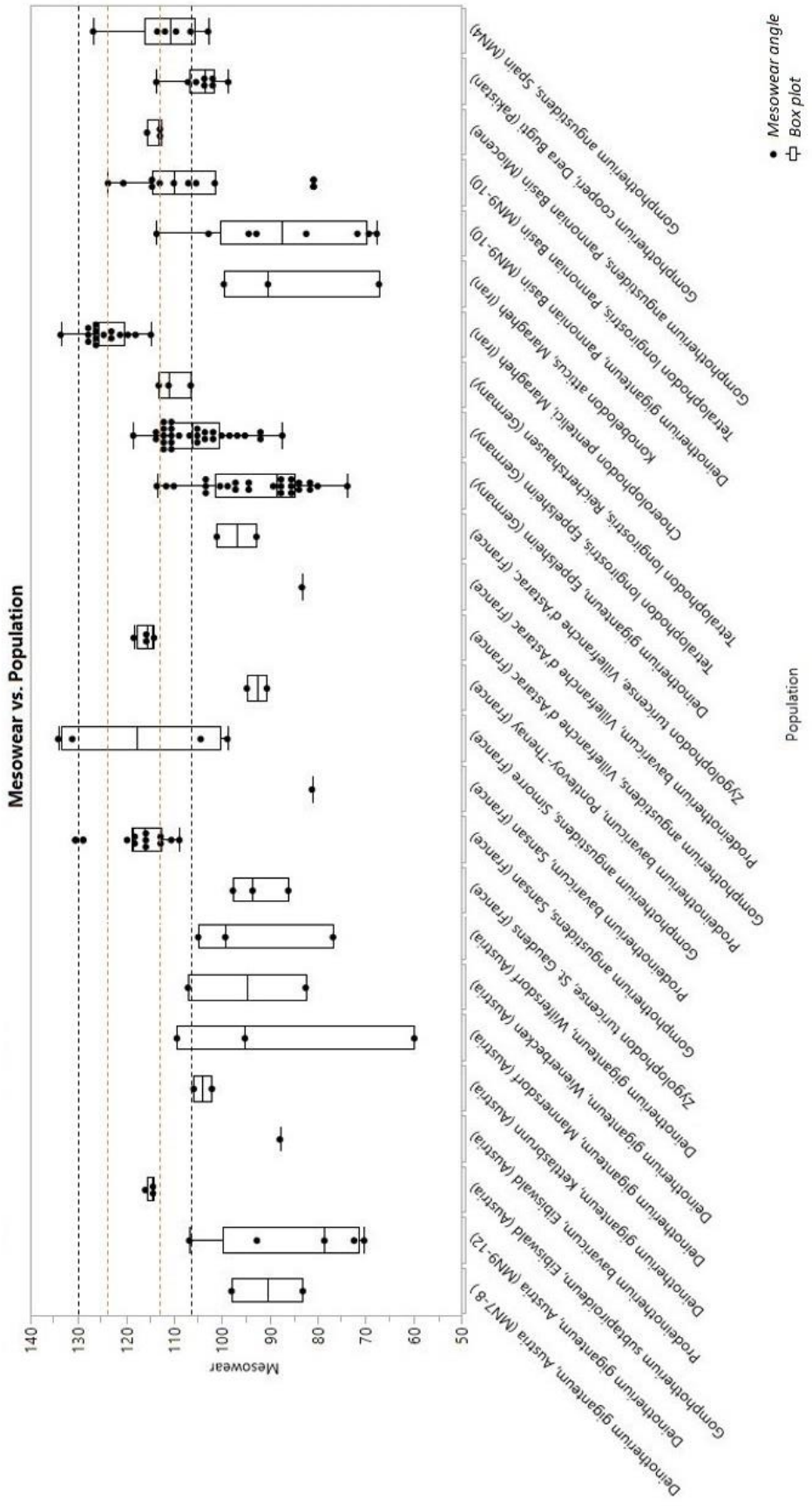


Figure 10. Comparison of the mean mesowear angles of the studied proboscideans. Proboscidean populations are organized into apathetical order according country and locality.

8.2 PALEOCOMMUNITIES OF MIOCENE PROBOSCIDEANS

The results show that paleocommunities of proboscideans were common throughout the Europe and often consisted of more than two species. Details of each paleocommunity is showed in Table 2. Based on Wilcoxon signed-rank test, no significant difference was found for paleocommunities in Eibiswald, Sansan, Villefranche d'Astarac and Eppelsheim. However, the significantly different results of the paleocommunities of Maragheh and Pannonian basin were one of the most interesting findings, as further discussed in Section 9.

Table 2. Miocene paleocommunities with locality mean mesowear and locality mean hypsodonty value.

Paleocommunity	Species	Age	Locality mean mesowear	Locality mean hypsodonty
Eibiswald, Austria		MN 5	101,3	1,2
	Gomphotherium subtapiroideum			
	Prodeinotherium bavaricum			
Eppelsheim, Germany		MN 9	98,9	1,19
	Deinotherium giganteum			
	Tetralophodon longirostris			
Maragheh, Iran		MN 12	105	1,91
	Choerolophodon pentelici			
	Konobelodon atticus			
Pannonian Basin, Austria		MN 9 - MN 10	96,5	1,2
	Gomphotherium angustidens			
	Deinotherium giganteum			
	Tetralophodon longirostris			
Sansan, France		MN 6	99,2	1
	Gomphotherium angustidens			
	Prodeinotherium bavaricum			
Villefranche d'Astarac, France		MN 7 MN 8	98,7	1
	Gomphotherium angustidens			
	Prodeinotherium bavaricum			
	Zygolophodon turicensis			

Based on species specific diet as reconstructed above, the gomphotheres indicating mixed-feeding were according to my results likely the most common sympatric species throughout European paleocommunities. As Table 2 shows, gomphotheres (constituting *Choerolophodon*, *Gomphotherium, Konobelodon* and *Tetralophodon*) were present in all communities. The results indicated that gomphotheres were likely accompanied with species preferring browsing diets, as that is the case with *Prodeinotherium bavaricum* in the paleocommunities in Eibiswald and Sansan. In the paleocommunity in Villefranche d'Astarac, these were further accompanied by another browser, *Zygolophodon turicensis,* indicating possibly the presence of interspecific competition. Likely the small sample size of *Prodeinotherium bavaricum* and *Zygolophodon turicensis* defected to the significance of the results.

Furthermore, the paleocommunity of Eppelsheim constituted two browsing species of *Deinotherium giganteum* and *Tetralophodon longirostris,* which statistically insignificant differences suggest similarity in the feeding preferences and possibly, thus indicating equity in the habitats, such as likely forest dominated vegetation, commonly connected with browsing diets (Kaiser et al., 2013). On the other hand, the *Tetralophodon* shows significant variation in mean mesowear angles.

Notably, the paleocommunity of Maragheh comprised *Choerolopodon pentelici* for which grazing diet is indicated, accompanied with browsing *Konobelodon atticus*. The significant result of this paleocommunity indicates a dietary niche separation of these sympatric species, for illustration see Figure 11. In contrast to the paleocommunity in Eppelsheim, *Deinotherium giganteum* and *Tetralophodon longirostris* in Pannonian basin (MN9 – MN 10) paleocommunity, were found to indicate a significant difference in feeding preferences. Despite that average mean mesowear angels indicate closely structured niches between the *D. giganteum* (93 ˚) indicating browsing and *T. longirostris* (105 ˚) implying browse-dominant mixed-feeding, the comparison in the Figure 11, clearly shows that medians of each populations don't overlap and *T. longirostris* has higher flexibly towards pure mixed-feeding, thus suggesting clear difference in dietary niches after all.

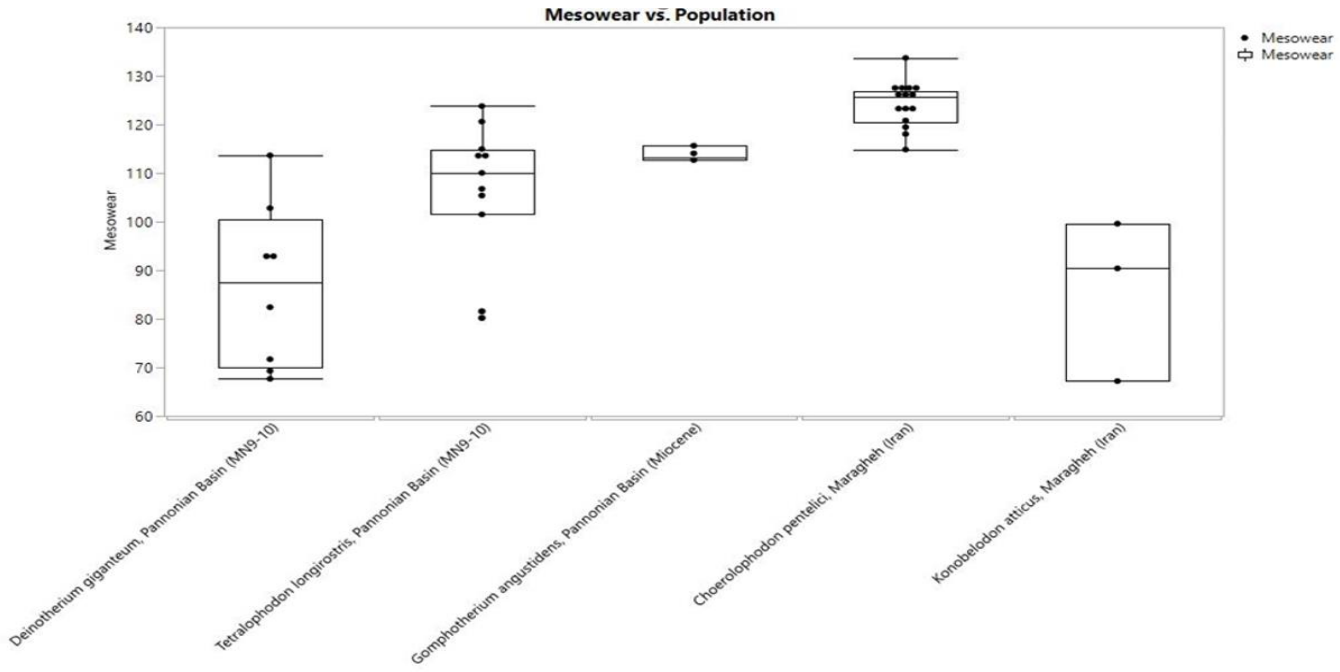
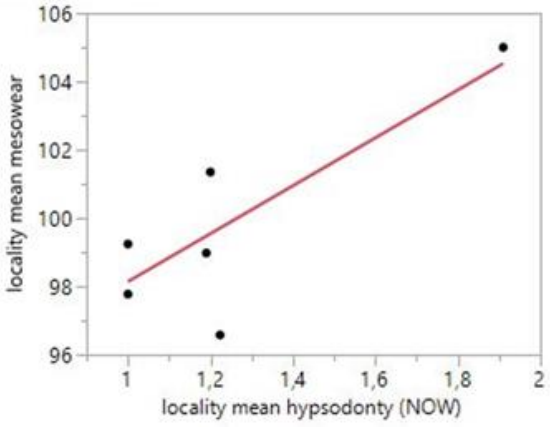


Figure 11. Comparison of the significant paleopopulations of the Miocene proboscideans.

8.3 VEGETATION PATTERNS AND ENVIRONMENT CHARACTERISTICS

The paleobotanical findings demonstrated that sites in Pannonian basin are clearly dominated by forested environments. According to Utescher et al. (2017) the Pannonian basin was found to be dominated by temperate broadleaf vegetation as herbs and grasses were particularly absent. The broadleaf deciduous vegetation persisted throughout the epoch, with variables diversities conifers and broadleaf evergreen vegetation (Utescher et al., 2017). Interestingly, the Maragheh, based on phytolith data, show considerable grass-dominated vegetation, perhaps as much as 75%, further complemented with woodland mosaic patterns (Strömberg et al., 2007).

Furthermore, the linear regression of mean mesowear angles and locality mean hypsodonty values showed statistically significant results of $p>0,0248$. As shown in Figure 12, the locality mean mesowear angles and locality mean hypsodonty values show positive correlation indicating relationship between the environment conditions and the diet. These results are further discussed in Section 9.



Summary of Fit

RSquare	0,667719
RSquare Adj	0,601262
Root Mean Square Error	1,747309
Mean of Response	99,66785
Observations (or Sum Wgts)	6

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	1	30,675890	30,6759	10,0475
Error	5	15,265445	3,0531	Prob > F
C. Total	6	45,941336		0,0248*

Parameter Estimates

Term	Estimate	Std Error	t Ratio	Prob>|t|
Intercept	91,120813	2,776113	32,82	<,0001*
locality mean hypsodonty (NOW)	7,0194647	2,214497	3,17	0,0248*

Figure 12. Linear regression of locality mean mesowear angles and locality mean hypsodonty value. Note the positive correlation with statistically significant results (p-value > 0.0248).

9 DISCUSSION

The purpose of this study was to reconstruct the feeding preferences of the studied proboscidean genera with first goal of analysing the occlusal surfaces for determining the general abrasiveness of the diet based on dental wear. The second goal was to provide estimations of the vegetation patterns and environment characteristics based on dental mesowear as ecometric tool, discussed in Section 9.4. With respect to the first research goal, it was found that the relative amounts of attrition and abrasion dominant dental wear on proboscideans allows differentiating the diets of the species (Saarinen & Lister, 2016). The diets were interpreted according to parameters given in Saarinen et al. (2015), with sharp angles (<106 ˚) reflecting low amounts of grass in the diet (browser, <10% of grass) and blunt (>130 ˚) mesowear angles indicating significant components of grass in the diet (grazer, >90% of grass). The results provide insight to the Miocene proboscideans diets, as the majority of the species were browsers without any grass compound in their diet. Furthermore, the results provide a general trend increasing the numbers of relatively grazing-adapted species and decline of browsing species during the Miocene epoch, as found in previous studies (Cerling et al., 1999; Janis, 1993; Saarinen, 2019). Notably, authors found that proboscideans, expect deinotheres, show fundamental shift into grazing diets after the Miocene epoch, likely due the changes in the landscapes, as discussed in Section 3.

The results support the view that grazers have a tendency to have abrasion-dominated occlusal surfaces in the open and arid conditions where open-adapted grasses are abundant, whereas browsers tend to be more attrition-dominated in forest environments with closed canopy (Kaiser et al., 2013). Observed differences in the mesowear angles, and thus in the diet, are likely explained by differences in dominant vegetation in each locality. These differences are indirectly linked to a higher hypsodonty value in more arid and open environments. These results show similar indications that craniodental morphologies correlate with known environment and vegetation changes in the Miocene (Semprebon et al., 2004). The uplifts of Alpine and Himalayan ranges, and changes in ocean currents, increased continentality that contributed cooler and more seasonal climate that led to the replacement of forest vegetation in many study localities (Calandra et al., 2008, 2010; Fortelius et al., 2002; Janis, 1993). Calandra et. al (2008) suggested that this would have provided more diversified environments and thus larger selection of niches, that in turn allowed higher diversification of proboscideans (Shoshani & Tassy, 2005). Furthermore, Saarinen (2019) indicated that seasonal semi-open woodland environments supported such large sized browsers as the *Deinotherium* and *Tetralophodon*. Thus, diet is clearly a bridge between the habitats and morphologies, related to notable differences in vegetation.

9.1 DEINOTHERIIDAE

Deinotherium giganteum shows attrition-dominant wear facets with on average sharp mean mesowear angles (see Table 1), thus indicating pure browsing diets. Hence, consistent with the microwear studies of Calandra et al. (2008, see introduction), the simple lophodont tooth patterns of *D. giganteum* allowed utilization of soft dicotyledonous foliage without any grass-component in the diet (Calandra et al., 2008). Furthermore, for *Prodeinotherium bavaricum*, which were a conservative taxon of the deinotheres lineage, results suggest similarly weakly abrasive, and thus browsing, diet. For deinotheres it is typical to shear on plant material in mastication, which in turn sustains the cutting edges of the molars through different dental wear angles (Cerling et al., 1999). Hence, this is commonly considered as explanatory cause for the outstanding difference of deinotheres which were the only proboscideans that did not develop horizontal displacement, as discussed in Section 5.1 (Cerling et al., 1999; Göhlich, 1999). Thus, the observed high variation in mesowear angles of *Deinotherium giganteum,* might result from the small sample size, or alternatively the differences in shearing motion between individuals. However, this would require further studies.

These findings are in line with previous studies that have found that deinotheres remained browsers regardless of timing, species, or environmental characteristics (Cerling et al., 1999; Markov et al., 2001; Saarinen et al., 2015). According to modern understanding, the direct ancestors of deinotheres are

unknown, and thus the species seems to appear from nowhere and after existing for about 20 million years the entire lineage disappeared without being divided into numerous phyletic lines nor significantly changing in appearance, except for their size (Markov et al., 2001). According to Göhlich (1999), within the *Prodeinotherium-Deinotherium*-lineage the body-height increased from circa 2,5 m. to 4 m., thus ending up with some of the largest land mammals of the Neogene. Instead, the craniodental characteristics remained largely unchanged (Cerling et al., 1999). Hence, authors have suggested that deinotheres were well adapted to their niche of closed forests and had a highly specialized diet on tree vegetation, likely higher tree branches, based on their size and craniodental features (Markov et al., 2001). Likewise, Calandra et al. (2010) concluded *Deinotherium giganteum* were tied ecologically into wet woodlands with enough tree vegetation to feed on, which has the tendency to correlate with browsing diet in general. Later, along the Miocene climate and environment changes (Eronen et al., 2010; Herbert et al., 2016) deinotheres assumingly inhabited remaining hygrophilous forests and forest patches (Markov et al., 2001) and thus disappeared along the rise of modern vegetation patterns in the Miocene-Pliocene transition (Herbert et al., 2016; Semprebon et al., 2004).

9.2 GOMPHOTHERIIDAE

Unlike Deinotheriidae, gomphotheres show slightly blunter mesowear angles, but also significant differences between and within species, as shown in Table 1. The results clearly demonstrate the shift in the feeding preferences of gomphotheres prior to Miocene climate change. In the western parts of the Europe, *Gomphotherium angustidens* results show browse-dominated diet in the Early Miocene, that shifted into mixed-feeding in the Middle Miocene. In Central Europe, the results suggest that G. *angustidens* remained as mixed-feeder throughout the Miocene epoch.

The difference between Western and Central-Europe is likely due to the differences in environmental conditions, and hence the vegetation. According to previous studies (Eronen et al., 2010; Fortelius et al., 2002) based on hypsodonty values and ecomorphological characteristics, the Iberian peninsula transformed from generally humid conditions of the Early Miocene into very dry conditions of the Late Miocene, whereas Central-Europe remained relatively humid throughout the Miocene when compared to rest of the Eurasia (Eronen et al., 2010). Nevertheless, the previous studies have indicated a clear decrease in precipitation in Eurasia on a wide scale as the Late Miocene took place (Eronen et al., 2010; Fortelius et al., 2002; Ivanov et al., 2010). Additionally, according to Cerling et al. (1999), during the Miocene epoch, C_4 -grasses were restricted into tropical and subtropical regimes with rain during the warm growth season. Thus, the cooler climate regimes throughout Northern Eurasia and relatively arid regions of the Mediterranean would have precluded C_4-vegetation (Eronen et al., 2010), thus proboscideans in Western

Europe were therefore likely to have strictly C_3-based diets (Cerling et al., 1999). Hence, the conditions of the Early Miocene might have supported forest vegetation in Spain, as Agustí & Antón (2002) suggested for tropical and subtropical forest vegetation as high of 52 ˚N latitude at that time, supported by Böhme (2003). These indications likely explain the found browse-dominated feeding preference of *Gomphotherium angustidens* from Spain.

Thus, it can be postulated that the general trend of increased aridity during the Middle and Late Miocene Europe (Fortelius et al., 2002; Ivanov et al., 2010) would have enhanced the selection for flexible feeding abilities in newly appeared semi-open woodlands (Agustí & Antón, 2002), and thus favoured the mixed-feeding preferences for gomphotheres in the Central-Europe. This is further supported by the findings of Calandra et al. (2008) which suggested that mixed-feeding capabilities of gomphotheres allowed switching between habitats depending on the environmental conditions, competition and food availability. Furthermore, due to the large morphological diversification of the gomphotheres, see Section 4, these species probably fed on a large spectrum of vegetation (Calandra et al., 2008; Göhlich, 1999). This view is supported by the observations regarding the gomphotheres unspecialized bunodont dentition, that is better adapted for crushing and grinding, rather than cutting such as deinotheres lophodont dentition (Cerling et al., 1999). Hence, gomphotheres have shown tendency to increase in molar complexity and crown height during their 15 Ma long evolution, that would have allowed utilization of more abrasive foods (Cerling et al., 1999; Göhlich, 1999). Taken together, the significant changes in the landscapes drove a shift in the feeding preferences of gomphotheres, that likely was reinforced by the wide dietary niche. This would be the case in the population of *G. angustidens* from the Middle Miocene locality of Villefranche d'Astarac (France), that showed more abrasion-dominated mesowear angles and thus clear signal of mixed-feeding, for details see Table 1.

Interestingly, *Gomphotherium subtapiroideum* showed intermediate mean mesowear angles indicating mixed-feeding in Central-Europe already during the Early Miocene. The difference to the *G. angustidens* populations is likely explained by the ecological differences of these species. This finding is consistent with Calandra et al. (2010) who found that *G. subtapiroideum* did not show significant shift in the feeding preferences during the Early - and Middle Miocene sub epochs. This result suggested that *G. subtapiroideum* favoured the open woodlands. Hence, the changes of Miocene landscapes into more open and patchier (Strömberg et al., 2007), would not have assumingly as such significant effects on the ecology of this species in question, as it did for other gomphotheres tied to more closed forest patches (Calandra et al., 2010).

However, one interesting finding was the difference between the G. *angustidens* populations of the Middle Miocene from the localities of Sansan and Simorre. Despite occurring during same period with

geographically close localities, the population in Sansan indicated mixed-feeding. Instead, the population in Simorre indicated clear signal of pure browsing. This difference might be explained by small sample size from locality of Simorre. Yet, based on the indications of Calandra et al. (2008) this finding can be truly interesting difference that can be hypothetically discussed to indicate a significant difference in feeding preferences of two populations due the intraspecific competition. According to Calandra et al. (2008) the several genera belonging to Elephantoidea occupied Western-Eurasia from the late Early-Miocene until the end of epoch. Among them was another gomphothere, *Archaeobelodon filholi,* present in locality of Sansan, yet absent in Simorre (Calandra et al., 2008). Thus, further studies are required to consider whether the presence of closely related species in Sansan, drove the more flexible feeder of *G. angustidensis,* as discussed above, into more mixed-feeding diet. Furthermore, this view is supported by both micro- and mesowear studies that confirm the partitioning of available food resources i.e. niche separation of gomphotheres in order to avoid direct food competition (Calandra et al., 2008, 2010; Rivals & Lister, 2016; Saarinen & Lister, 2016). Likewise, *Gomphotherium cooperi* in the Early Miocene followed similar pattern by implying the browsing diet in Southern Asia, connected to generally humid conditions in the region (Fortelius et al., 2002; De Franceschi et al., 2008).

Tetralophodon longirostris showed diets ranging from browse to browse-dominated mixed-feeding and is in line with previous studies. *Tetralophodon* are a paraphyletic group in gomphotheres phylogeny of which is not fully established. *Konobelodon atticus* was recently taxonomically reidentified as an amebelodontine gomphothere (Konidaris et al., 2014), previously most commonly referred as *Tetralophodont atticus.* The significant differences in the diet of this species and further of C*hoerolophodon pentelici* are found to be best explained by vegetation patterns drawn from literature, as discussed below.

However, according to Wang et al. (2017) these large herbivores were dominant in the Late Miocene Europe. The diet of *Tetralophodon longirostris* is considered to connect with humid and flush environments found in the Molasse basin which extends largely to modern France, Switzerland, Germany and Austria during the Late Miocene (Eronen & Rössner, 2007). Eronen et al. (2007) indicated that the mixed feeders of the genera *Gomphotherium* and *Tetralophodon,* were major part of the mammal community in the Molasse basin. The area was characterized by a common wetland type, where the hinterlands were forests and woodlands and existent abundant water bodies were surrounded by riparian vegetation (Eronen & Rössner, 2007). Floodplains associated with the water bodies had seasonally varying grass cover that was suggested to increase extensively in the proportion of hard-to-digest fibrous plants (Eronen & Rössner, 2007). Such an environment certainly supported many different dietary adjustments of *Tetralophodon* (Calandra et al., 2008; Eronen & Rössner, 2007), supported by my results.

The high variation of mesowear angels within the *T. longirostris* showed flexibility in feeding, as in G. *angustidens,* which can suggest a similar pattern of seasonal variation in the diets, as found in modern elephants (Sukumar & Ramesh, 1992). Previous studies have found that modern elephants adjust their diets based on available vegetation (Cerling et al., 1999; Saarinen et al., 2015). For example, the African savanna elephant essentially has pure browsing diet in forested environments and more broadly mixed-feeding in more open savannas (Cerling et al., 1999). According to Saarinen & Lister (2016), the seasonal variation of modern elephants is in line with the extinct proboscideans' (*Mammuthus* and *Anancus*) ability for flexible feeding as grazers in open and dry environments and to adjust in woody environments to more browsing.

9.3 MAMMUTIDAE

Zygolophodon turicensis was one of the first species to reach the Europe as land bridge from Africa emerged (Agustí & Antón, 2002). This species is characterized with zygodont molars evolved sharp ridges that are more effective for cutting relatively more fibrous foods than bunodont (Göhlich, 1999). The results indicated browsing diets, indicating similar pattern as in studies compromising other Mammutidae species, such as the Pliocene *Mammut borsoni* from England (Saarinen & Lister, 2016) and microwear studies related to the American Mastodon (*Mammut americanum*) (Rivals, 2012).

9.4 ENVIRONMENTS AND VEGETATION

The second goal of this study sought to determine the relationship of the environmental conditions and vegetation patterns to characteristics of proboscideans diet. Hence, the obtained locality mean hypsodonty values are compared against the measured mesowear angles, as average hypsodonty in ungulate communities is considered to be ta proxy that correlates with precipitation patterns (Fortelius et al., 2002; Eronen et al., 2010). Hypsodonty value refers to the ratio of unworn molar height to its length or width (Janis, 1988). Thus, hypsodonty reflects the feeding adaptations, i.e. the foods the species have been adapted to utilize during its evolutionary history, rather than mesowear which indicates the feeding preferences i.e. what species did feed on during the lifetime (Kaiser et al., 2013). Hypsodonty as a proxy of precipitation is based on the observation that herbivores feeding close to ground, in open and dry environments, tend to have highly hypsodonty dentition regardless the species-specific diet (Janis, 1988; Fortelius et al., 2002; Ungar, 2015). Instead, those species feeding in moist and closed-canopy environments, tend to have the lowest molar crowns (Kaiser et al., 2013). Thus, hypsodonty is observed commonly in grazing herbivores, such as modern horses and elephants (Saarinen, 2008). Hence, high molar

crowns are commonly interpreted to reflect the adaption into highly abrasive diets and environments tied to these diet characteristics (e.g. Eronen et al., 2010; Kaiser et al., 2013; Mendoza et al., 2002).

Furthermore, the initial interpretation regarded hypsodonty as response to the spread of grass-dominated vegetation, yet more recent studies have suggested that hypsodonty was more closely related to general aridity of the environments resulting from more abrasive plants common in such environments (Fortelius et al., 2002; Strömberg et al., 2007). Thus, for the coincidence between hypsodonty, grazing and arid environments has been debated similarly to the ultimate cause of the dental wear, as discussed in Section 5.2. Nevertheless to the ultimate cause, not all grazers have hypsodonty dentition, thus separating the hypsodonty value from direct diet interpretations. Yet, the interpretations of hypsodonty values allow me to evaluate the general characteristics of the herbivores habitats as discussed below. In previous studies the average hypsodonty values in ungulate communities have been shown to correlate with the amount of precipitation (Eronen et al., 2010; Fortelius et al., 2002). In general, the value of 1 is considered to indicate very humid conditions with increasing in scale of 0,3. Every increase in the scale reflects lower general humidity of the environment thus, on average, the hypsodonty value of 1,6 indicates significant increase in aridity (Fortelius et al., 2002).

The comparison of locality mean hypsodonty and locality mean mesowear angles of paleocommunities in the Early Miocene, showed for browsers, yet commonly found in moist and forested habitats, on average a hypsodonty value of 1. Slightly higher hypsodonty values were shown for Central-Europe localities c. 1,2 with browsing preferences respectively, which is supported by Fortelius et al. (2003) that suggested humid conditions for throughout Eurasia. As discussed before, *Gomphotherium subtapiroideum* stands out with mixed-feeding preference due the ecological differentiation, despite the humid conditions indicated by hypsodonty values. Furthermore, both studies of Fortelius et al. (2003) and Eronen et al. (2010) showed the slight increase of aridity during the Middle Miocene, reflected further by a shift in feeding preferences of *G. angustidens* populations, despite the largely similar hypsodonty values of on average of 1.

However, during the Late Miocene, the locality mean hypsodonty value shows statistically significant differences between the feeding preferences of the proboscideans. Browsing and browse-dominated mixed-feeding of the paleocommunities in Pannonian basin localities correlates with hypsodonty value of 1,2, indicating relatively humid conditions, yet less humid than in the Early Miocene. As the results showed the significant difference of feeding preferences of *Deinotherium giganteum* and *Tetralophodon longirostris*, the Pannonian basin environment likely supported high variation in the vegetation patterns, supported by the hypsodonty value, thus allowing the found larger variation in *Tetralophodon longirostris* feeding preferences in the Pannonian basin paleocommunity than in the Eppelsheim's paleocommunity.

Thus, it can be suggested that *T. longirostris* expansion into direction of domination of the mixed-feeding preferences likely favoured the co-existence of these two sympatric species. Additionally, the *Gomphotherium angustidens* with pure mixed-feeding in Pannonian basin is likely biased result due the small sample size and discontinuity in timing.

Instead, in the paleocommunity in Maragheh, the hypsodonty value is significantly higher, c. 1,9, correlating with grass-dominant mixed-feeding for *Choerolophodon pentelic*i. Furthermore, the existence of the *Konobelodon atticus* with indication of browsing diet, suggest that both grass vegetation and forest or woodland vegetation was available in the habitat. This observation is supported by Fortelius et al. (2002) which demonstrated that the arid, and thus more open environments, spread from Western-Asia towards Europe during the Late Miocene. Thus, *Choerolophodon* diet essentially reflects the gradual spread of grasslands in Western Eurasia at that time (Strömberg et al., 2007).

However, despite the common observation of correlation between the locality mean hypsodonty value and several environmental factors (Eronen et al., 2010; Janis, 1988; Kaiser et al., 2013; Mendoza et al., 2002), the correlation of the locality mean hypsodonty value and mesowear angle does not directly tell which of these environmental factors explains the observed variation in the mesowear angles. Hence, it can be stated that mesowear as ecometric tool is correlated with the proxy of general openness and aridity (locality mean hypsodonty), but the mechanism of how it is correlated with the proboscidean dietary signal is not explained by this analysis. Thus, further studies are required in order to test directly the amount of grass in the environment through the comparison of pollen records of *Graminea* and *Poaceace*- groups, to show correlation between mesowear angles and amount of grass in the diet. Due the lack of data, this was a challenge for this study.

Consequently, this finding is noteworthy as grasses are considered to better tolerate seasonal drought, frequent fires, and heavy grazing than woodland vegetation (Saarinen et al., 2020). Especially the appearance of C4-plants, which are well adapted to warm, dry, and open environments (as discussed in Section 3) are considered to have increased in abundance during the Late Miocene, yet with strong and complex temporal and spatial variations and fluctuations (Cerling et al., 1993; Saarinen et al., 2020; Strömberg & McInerney, 2011; Strömberg et al., 2007). Based on the trend of hypsodonty values during Late Miocene Eurasia, the more arid and open environments likely favoured the grass-dominant vegetation when compared to general woodlands patterns. Hence, the hypsodonty values reflect the general humidity of the studied proboscidean communities in which the general openness of these habitats can be inferred. Thus, the differences in the mean mesowear angles is likely due the ratio of the grass-dominant vegetation in the study localities, that is indirectly linked to the locality mean hypsodonty values, as discussed next.

The study of Utescher et al. (2017) from Pannonian basin and Strömberg et al. (2007) from Maragheh provided sufficient context to discuss the paleoclimatic characteristics and patterns of paleovegetation in these two localities. These latest results reconstructed woodland-dominated wetlands in Pannonian basin and grass-dominated mosaic vegetation for locality of Maragheh, which are in line with my results. Both showed similar trend in regional response to Miocene global cooling, migration of shoreline and extent of open woodland areas.

The Pannonian basin localities studied here have been dated as representing the Late Miocene based on floral records deposited into ancient lake sediments (Utescher et al., 2017). The findings of this study indicated broadleaved deciduous vegetation as dominant pattern with minor broadleaf evergreen and coniferous components (Utescher et al., 2017). Furthermore, around the lowlands of the past lakeshore and in surrounding fluviatile facies, the records suggested wetland characteristics. The authors suggested that the retreat of the coastline at 6.5 Ma favoured the expansion of swamp forest vegetation. According to Utescher et al. (2017) these observations were supported by previous plant-based reconstructions and the overall humid and warm conditions interpreted from the paleobotanical records. Instead, in the late Late-Miocene the broadleaved evergreen components showed a decreasing trend. According to Utescher et al. (2007), the observed trends were in line with studies of Cerling et al. (1997) and Strömberg et al. (2011) which showed that in large areas in Europe, including the Mediterranean region and Western Asia environments gradually changed from forests and woodlands into increasingly open savannas and grasslands.

Strömberg et al. (2007) used phytolith assemblages to consider the association of paleovegetation structure, regarding open and closed habitats, to fauna characteristics. Phytoliths and other biogenic silica bodies were extracted from the sediment samples from Greece, Turkey and Iran. These authors were able to show that during the Miocene these localities had diverse assemblages of short celled grass phytoliths typical for open-habitat grasses. Instead, some indications of forest phytoliths was found, but were significantly rarer than in the Eocene. According to Strömberg (2007) these findings are consistent with carbon isotope records of paleosols and tooth enamel. Likewise, according to Strömberg et al. (2007) a wealth of evidence based on macro- and palynoflorar records primarily documented the tropical and subtropical evergreen broad-leaved forests to give in during the Miocene to temperate forests dominated by deciduous angiosperms and conifers in Western Eurasia. Respectively in Southern and Eastern Europe the subtropical landscapes shifted into scrub-dominated forests and woodlands with regional variation from humid to dry overall conditions. Overall, the observed grazing in Maragheh's *Choerolophodon* clearly reflects the phytolith-based interpretation of the abundance of the grass dominant vegetation in the

particular environment, while the browse-dominated dietary signals from other proboscidean communities reflect the more wooded environments.

10 CONCLUSIONS

The diets of the Miocene (23 - 5 Ma) proboscideans from Eurasia were inferred from mesowear angle measurements, allowing the reconstruction of key environmental parameters and vegetation patterns. As a conclusion, the positive correlation between mesowear and locality mean hypsodonty suggests that the proboscidean communities' diets were, on average, more grass-dominated in localities where higher hypsodonty values indicated more open and arid environments. In addition, the vegetation data shows that there was indeed more grass-dominated vegetation in such environments with clearly higher hypsodonty values e.g. the locality of Maragheh. Taken together, the results indicate that feeding with significant grass components in the diet is a result of grass-dominated vegetation patterns (based on the high proportion of grass based phytoliths) in the habitat due the general aridity of the environment (based on the high hypsodonty values). Respectively, browsing was common in more humid environments with lowest hypsodonty values, due to the dominant forest vegetation patterns.

Thus, this study has identified that proboscideans were diverse and abundant with significant differences in feeding preferences varying from browsing deinotheres, the browse-dominated or mixed-feeding of gomphotheres, to partially grazing of *Choerolophodon.* The found shift in feeding preferences of the proboscideans is clearly tied to fluctuations of the environment prevailing in the Miocene epoch, a trend that led to modern elephants grazing diets and hypsodonty molars. The results of this study are supported by previous paleoecological studies (Calandra et al., 2008; Cerling et al., 1999; Saarinen, 2019; Saarinen et al., 2015). Thus, this study has shown a clear relationship between the long evolutionary trends of changes in dental morphologies and the environment characteristic of the habitat, through the diet composition. These findings suggest that differences in feeding preferences allowed the sympatric proboscideans to co-exist without outcompeting each other by partitioning the ecological niches. Conclusively, fossilised dental wear reflects vegetation, environment conditions, and ultimately climate at a given time at given deposit locality (Fraser & Theodor, 2011; Saarinen et al., 2015).

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APPENDIX 1

Statistically significant differences between the proboscidean populations.

Population	- Population	Difference	Std Err Dif.	p-value
Gomphotherium subtapiroideum, Eibiswald (Austria)	Deinotherium giganteum, Austria (MN9-12)	3,7333	1,788854	0,0369
Prodeinotherium bavaricum, Pontlevoy-Thenay (France)	Gomphotherium angustidens, Sansan (France)	-6,7083	3,195048	0,0358
Gomphotherium angustidens, Sansan (France)	Deinotherium giganteum, Austria (MN7-8)	6,7083	3,195048	0,0358
Gomphotherium angustidens, Sansan (France)	Deinotherium giganteum, Austria (MN9-12)	8,3583	2,687936	0,0019
Gomphotherium angustidens, Sansan (France)	Deinotherium giganteum, Kettlasbrunn (Austria)	6,7083	3,195048	0,0358
Gomphotherium angustidens, Sansan (France)	Deinotherium giganteum, Mannersdorf (Austria)	6,875	2,886751	0,0172
Gomphotherium angustidens, Sansan (France)	Deinotherium giganteum, Wienerbecken (Austria)	6,7083	3,195048	0,0358
Gomphotherium angustidens, Sansan (France)	Deinotherium giganteum, Wilfersdorf (Austria)	7,2917	2,886751	0,0115
Gomphotherium angustidens, Sansan (France)	Zygolophodon turicensis, St. Gaudens (France)	7,2917	2,886751	0,0115
Gomphotherium angustidens, Simorre (France)	Gomphotherium angustidens, Sansan (France)	-7,2917	2,886751	0,0115
Gomphotherium angustidens, Villefranche d'Astarac (France)	Deinotherium giganteum, Austria (MN9-12)	4,275	1,837117	0,02
Zygolophodon turicensis, Villefranche d'Astarac, (France)	Gomphotherium angustidens, Sansan (France)	-6,7083	3,195048	0,0358
Tetralophodon longirostris, Eppelsheim (Germany)	Deinotherium giganteum, Austria (MN9-12)	12,6621	4,821387	0,0086
Tetralophodon longirostris, Eppelsheim (Germany)	Gomphotherium angustidens, Villefranche d'Astarac (France)	-15,2198	5,156573	0,0032
Tetralophodon longirostris, Eppelsheim (Germany)	Gomphotherium subtapiroideum, Eibiswald (Austria)	-14,7126	5,688229	0,0097
Tetralophodon longirostris, Eppelsheim (Germany)	Prodeinotherium bavaricum, Pontlevoy-Thenay (France)	13,0948	6,645757	0,0488
Tetralophodon longirostris, Eppelsheim (Germany)	Zygolophodon turicensis, St. Gaudens (France)	12,8736	5,688229	0,0236
Deinotherium giganteum, Eppelsheim (Germany)	Gomphotherium angustidens, Villefranche d'Astarac (France)	-14,355	4,583608	0,0017
Deinotherium giganteum, Eppelsheim (Germany)	Gomphotherium subtapiroideum, Eibiswald (Austria)	-13,8133	5,02409	0,006
Tetralophodon longirostris, Reichertshausen (Germany)	Deinotherium giganteum, Eppelsheim (Germany)	11,5733	5,02409	0,0212
Choerolophodon pentelici, Maragheh (Iran)	Deinotherium giganteum, Austria (MN7-8)	8,2167	3,801316	0,0307

Choerolophodon pentelici, Maragheh (Iran)	Deinotherium giganteum, Austria (MN9-12)	9,8667	3,05505	0,0012
Choerolophodon pentelici, Maragheh (Iran)	Deinotherium giganteum, Kettlasbrunn (Austria)	8,2167	3,801316	0,0307
Choerolophodon pentelici, Maragheh (Iran)	Deinotherium giganteum, Mannersdorf (Austria)	8,8	3,376389	0,0092
Choerolophodon pentelici, Maragheh (Iran)	Deinotherium giganteum, Wienerbecken (Austria)	8,2167	3,801316	0,0307
Choerolophodon pentelici, Maragheh (Iran)	Deinotherium giganteum, Wilfersdorf (Austria)	8,8	3,376389	0,0092
Choerolophodon pentelici, Maragheh (Iran)	Gomphotherium angustidens, Sansan (France)	7,875	3,074085	0,0104
Choerolophodon pentelici, Maragheh (Iran)	Gomphotherium angustidens, Simorre (France)	8,8	3,376389	0,0092
Choerolophodon pentelici, Maragheh (Iran)	Gomphotherium angustidens, Villefranche d'Astarac (France)	8,075	3,166667	0,0108
Choerolophodon pentelici, Maragheh (Iran)	Gomphotherium subtapiroideum, Eibiswald (Austria)	8,4	3,376389	0,0129
Choerolophodon pentelici, Maragheh (Iran)	Prodeinotherium bavaricum, Pontlevoy-Thenay (France)	8,2167	3,801316	0,0307
Choerolophodon pentelici, Maragheh (Iran)	Tetralophodon longirostris, Reichertshausen (Germany)	8,8	3,376389	0,0092
Choerolophodon pentelici, Maragheh (Iran)	Zygolophodon turicensis, St. Gaudens (France)	8,8	3,376389	0,0092
Choerolophodon pentelici, Maragheh (Iran)	Zygolophodon turicensis, Villefranche d'Astarac, (France)	8,2167	3,801316	0,0307
Konobelodon atticus, Maragheh (Iran)	Choerolophodon pentelici, Maragheh (Iran)	-8,8	3,376389	0,0092
Konobelodon atticus, Maragheh (Iran)	Gomphotherium angustidens, Sansan (France)	-7,2917	2,886751	0,0115
Konobelodon atticus, Maragheh (Iran)	Tetralophodon longirostris, Eppelsheim (Germany)	-13,2414	5,688229	0,0199
Gomphotherium cooperi, Dera Bugti (Pakistan)	Choerolophodon pentelici, Maragheh (Iran)	-11,4042	2,968554	0,0001
Gomphotherium cooperi, Dera Bugti (Pakistan)	Deinotherium giganteum, Austria (MN7-8)	4,6875	2,386304	0,0495
Gomphotherium cooperi, Dera Bugti (Pakistan)	Deinotherium giganteum, Austria (MN9-12)	4,3875	2,217121	0,0478
Gomphotherium cooperi, Dera Bugti (Pakistan)	Deinotherium giganteum, Eppelsheim (Germany)	10,8075	3,926473	0,0059
Gomphotherium cooperi, Dera Bugti (Pakistan)	Deinotherium giganteum, Pannonian Basin (MN9-10)	5,375	2,378725	0,0238
Gomphotherium cooperi, Dera Bugti (Pakistan)	Gomphotherium angustidens, Sansan (France)	-9,0625	2,699293	0,0008
Gomphotherium cooperi, Dera Bugti (Pakistan)	Gomphotherium angustidens, Villefranche d'Astarac (France)	-5,8125	2,204077	0,0084
Gomphotherium cooperi, Dera Bugti (Pakistan)	Gomphotherium subtapiroideum, Eibiswald (Austria)	-5,2708	2,240257	0,0186
Gomphotherium cooperi, Dera Bugti (Pakistan)	Konobelodon atticus, Maragheh (Iran)	4,8125	2,240257	0,0317

Gomphotherium cooperi, Dera Bugti (Pakistan)	Prodeinotherium bavaricum, Pontlevoy-Thenay (France)	4,6875	2,386304	0,0495
Gomphotherium cooperi, Dera Bugti (Pakistan)	Zygolophodon turicensis, St. Gaudens (France)	5,2708	2,240257	0,0186
Deinotherium giganteum, Pannonian Basin (MN9-10)	Choerolophodon pentelici, Maragheh (Iran)	-11,4042	2,969287	0,0001
Deinotherium giganteum, Pannonian Basin (MN9-10)	Gomphotherium angustidens, Sansan (France)	-9,0625	2,700309	0,0008
Deinotherium giganteum, Pannonian Basin (MN9-10)	Gomphotherium angustidens, Villefranche d'Astarac (France)	-5,8125	2,20794	0,0085
Deinotherium giganteum, Pannonian Basin (MN9-10)	Gomphotherium subtapiroideum, Eibiswald (Austria)	-5,2708	2,245366	0,0189
Deinotherium giganteum, Pannonian Basin (MN9-10)	Tetralophodon longirostris, Eppelsheim (Germany)	-11,5625	4,322225	0,0075
Gomphotherium angustidens, Pannonian Basin (Miocene)	Choerolophodon pentelici, Maragheh (Iran)	-8,4	3,376389	0,0129
Gomphotherium angustidens, Pannonian Basin (Miocene)	Deinotherium giganteum, Austria (MN9-12)	3,7333	1,788854	0,0369
Gomphotherium angustidens, Pannonian Basin (Miocene)	Deinotherium giganteum, Eppelsheim (Germany)	13,0667	5,02409	0,0093
Gomphotherium angustidens, Pannonian Basin (Miocene)	Tetralophodon longirostris, Eppelsheim (Germany)	13,6092	5,688229	0,0167
Tetralophodon longirostris, Pannonian Basin (MN9-10)	Choerolophodon pentelici, Maragheh (Iran)	-11,1879	3,036146	0,0002
Tetralophodon longirostris, Pannonian Basin (MN9-10)	Deinotherium giganteum, Austria (MN9-12)	5,8182	2,567867	0,0235
Tetralophodon longirostris, Pannonian Basin (MN9-10)	Deinotherium giganteum, Eppelsheim (Germany)	10,1455	3,810962	0,0078
Tetralophodon longirostris, Pannonian Basin (MN9-10)	Deinotherium giganteum, Pannonian Basin (MN9-10)	5,9375	2,614789	0,0232
Tetralophodon longirostris, Pannonian Basin (MN9-10)	Gomphotherium angustidens, Sansan (France)	-5,6629	2,831104	0,0455
Gomphotherium angustidens, Spain (MN4)	Choerolophodon pentelici, Maragheh (Iran)	-7,5833	2,997221	0,0114
Gomphotherium angustidens, Spain (MN4)	Deinotherium giganteum, Austria (MN9-12)	4,5833	2,008316	0,0225
Gomphotherium angustidens, Spain (MN4)	Deinotherium giganteum, Eppelsheim (Germany)	12,5033	4,132083	0,0025
Gomphotherium angustidens, Spain (MN4)	Deinotherium giganteum, Pannonian Basin (MN9-10)	5,3958	2,25924	0,0169
Gomphotherium angustidens, Spain (MN4)	Konobelodon atticus, Maragheh (Iran)	4,25	1,936492	0,0282
Gomphotherium angustidens, Spain (MN4)	Zygolophodon turicensis, St. Gaudens (France)	4,25	1,936492	0,0282

APPENDIX 2

Fossil specimens studied with the mesowear angles of each molar.

Specimen ID.	***Genus***	***Sp.***	**Locality**	**Mesowear angle**
927M	*Gomphotherium*	*angustidens*	Burgos	102,9
NHML M 11050 (CAST)	*Gomphotherium*	*cooperi*	Dera Bugti	113,7
NHML M 11051 (CAST)	*Gomphotherium*	*cooperi*	Dera Bugti	98,7
NHML M 12178 (DEXT.)	*Gomphotherium*	*cooperi*	Dera Bugti	103,6
NHML M 12178 (SIN.)	*Gomphotherium*	*cooperi*	Dera Bugti	107,1
NHML M 12179 (DEXT.)	*Gomphotherium*	*cooperi*	Dera Bugti	103,6
NHML M 12179 (SIN.)	*Gomphotherium*	*cooperi*	Dera Bugti	101,4
NHML M 12181	*Gomphotherium*	*cooperi*	Dera Bugti	102,5
NHML M 12194	*Gomphotherium*	*cooperi*	Dera Bugti	105,4
1939/0001/0022 / 1939NO10 I. 22	*Deinotherium*	*giganteum*	Eibestal bei Mistelbach	70,3
C. 3870 1882	*Gomphotherium*	*angustidens*	Eibiswald	113,2
M.S. NO 120-121	*Gomphotherium*	*subtapiroideum*	Eibiswald	114,6
NHMW 115 / M.S. NO15	*Gomphotherium*	*subtapiroideum*	Eibiswald	115,6
NHMW A4139	*Gomphotherium*	*subtapiroideum*	Eibiswald	114,2
2000Z0027/0000	*Prodeinotherium*	*bavaricum*	Eibiswald	87,9
1954/74 S.NF2 TAF VII FJ. 1	*Gomphotherium*	*angustidens*	Eichkogel	112,7
NHML 1275 (CAST)	*Deinotherium*	*giganteum*	Eppelsheim	73,8
NHML 1542 (CAST)	*Deinotherium*	*giganteum*	Eppelsheim	80
1835 IX 2 / 14F IN	*Deinotherium*	*giganteum*	Eppelsheim	81
NHML 1735 T (CAST)	*Deinotherium*	*giganteum*	Eppelsheim	81
NHML M 154	*Deinotherium*	*giganteum*	Eppelsheim	83,4
NHML 19432 F	*Deinotherium*	*giganteum*	Eppelsheim	84,4
NHML M 9573 (CAST)	*Deinotherium*	*giganteum*	Eppelsheim	85,1
NHML 1735 (CAST)	*Deinotherium*	*giganteum*	Eppelsheim	85,2
NHML 1274 (CAST)	*Deinotherium*	*giganteum*	Eppelsheim	86,1
NHML 1738 A (CAST)	*Deinotherium*	*giganteum*	Eppelsheim	87,4
NHML 1246 (CAST)	*Deinotherium*	*giganteum*	Eppelsheim	87,8
NHML 19432 A	*Deinotherium*	*giganteum*	Eppelsheim	87,8
NHML 19432 G	*Deinotherium*	*giganteum*	Eppelsheim	88,6

14 IJ. ALPA	*Deinotherium*	*giganteum*	Eppelsheim	94,4
NHML 1753	*Deinotherium*	*giganteum*	Eppelsheim	94,4
NHML M 154	*Deinotherium*	*giganteum*	Eppelsheim	96,6
NHML (UNLABELLED SKULL, CAST)	*Deinotherium*	*giganteum*	Eppelsheim	97,7
NHML M 157	*Deinotherium*	*giganteum*	Eppelsheim	98,8
NHML 21269	*Deinotherium*	*giganteum*	Eppelsheim	100,1
12 Q 70	*Deinotherium*	*giganteum*	Eppelsheim	103
15.A.	*Deinotherium*	*giganteum*	Eppelsheim	103,4
12 W 67	*Deinotherium*	*giganteum*	Eppelsheim	103,7
14 IJ. 8	*Deinotherium*	*giganteum*	Eppelsheim	110,1
12 Y. 71	*Deinotherium*	*giganteum*	Eppelsheim	111,6
12.O? 68	*Deinotherium*	*giganteum*	Eppelsheim	113,6
Q.D 47	*Tetralophodon*	*longirostris*	Eppelsheim	87,4
9B. 45	*Tetralophodon*	*longirostris*	Eppelsheim	91,5
1852 I S88	*Tetralophodon*	*longirostris*	Eppelsheim	92,4
1852 I S90	*Tetralophodon*	*longirostris*	Eppelsheim	95,2
NHML M 2936 (CAST)	*Tetralophodon*	*longirostris*	Eppelsheim	96,5
NHML M 2934 (CAST)	*Tetralophodon*	*longirostris*	Eppelsheim	97,8
NHML M 139	*Tetralophodon*	*longirostris*	Eppelsheim	100,1
NHML M 2944	*Tetralophodon*	*longirostris*	Eppelsheim	101,4
NHML 19435 D	*Tetralophodon*	*longirostris*	Eppelsheim	102,2
NHML 21485 (DEXT.)	*Tetralophodon*	*longirostris*	Eppelsheim	103,5
NHML M 2930	*Tetralophodon*	*longirostris*	Eppelsheim	103,5
NHML M 135	*Tetralophodon*	*longirostris*	Eppelsheim	104,4
NHML 21485 (SIN.)	*Tetralophodon*	*longirostris*	Eppelsheim	105,1
NHML 21266	*Tetralophodon*	*longirostris*	Eppelsheim	105,8
NHML M 2908 (CAST)	*Tetralophodon*	*longirostris*	Eppelsheim	106,3
NHML M 2907 (CAST) (SIN.)	*Tetralophodon*	*longirostris*	Eppelsheim	108,9
NHML (NO NR.)	*Tetralophodon*	*longirostris*	Eppelsheim	109,2
NHML (NO NR.)	*Tetralophodon*	*longirostris*	Eppelsheim	109,6
NHML M 2919 (CAST)	*Tetralophodon*	*longirostris*	Eppelsheim	109,7
NHML M 2933 (CAST)	*Tetralophodon*	*longirostris*	Eppelsheim	110,2
NHML M 356 (CAST)	*Tetralophodon*	*longirostris*	Eppelsheim	110,5
NHML 21846	*Tetralophodon*	*longirostris*	Eppelsheim	110,7
NHML 2927 (CAST)	*Tetralophodon*	*longirostris*	Eppelsheim	110,7

NHML M 2946 (CAST)	*Tetralophodon*	*longirostris*	Eppelsheim	110,8
NHML M 2921 (CAST)	*Tetralophodon*	*longirostris*	Eppelsheim	110,9
NHML M 2907 (CAST) (DEXT.)	*Tetralophodon*	*longirostris*	Eppelsheim	111
NHML M 2931 (CAST)	*Tetralophodon*	*longirostris*	Eppelsheim	112,7
9C. 46	*Tetralophodon*	*longirostris*	Eppelsheim	113,4
NHML M 2942	*Tetralophodon*	*longirostris*	Eppelsheim	118,5
2019/0170/0003	*Deinotherium*	*giganteum*	Inzersdorf	69,3
1925 NO. 24 / SK2726	*Deinotherium*	*giganteum*	Josefsberg bei Hollabrunn	72,4
IN DISPLEY, LARGE JAW	*Deinotherium*	*giganteum*	Kettlasbrunn	98
A.T.A 8646 / SK2724 B	*Deinotherium*	*giganteum*	Kettlasbrunn	105,9
A.T.A 8646 / SK2724 A	*Deinotherium*	*giganteum*	Kettlasbrunn	102,1
1973/1597/3	*Deinotherium*	*giganteum*	Kohfidisch	92,7
2000Z0038/0000	*Deinotherium*	*giganteum*	Laaerberg	67,6
SK2631	*Deinotherium*	*giganteum*	Leithagebirge	78,6
2000Z0015/0000	*Deinotherium*	*giganteum*	Mannersdorf	109,4
2000Z0031/0001 /SK2715	*Deinotherium*	*giganteum*	Mannersdorf	95,2
2000Z0020/0000 / SK2634	*Deinotherium*	*giganteum*	Mannersdorf	59,8
A 4809	*Choerolophodon*	*pentelici*	Maragheh	127,9
A4807 / MA R - 2377	*Choerolophodon*	*pentelici*	Maragheh	120,4
A4825 / MA R - 2382	*Choerolophodon*	*pentelici*	Maragheh	118,1
MA R - 2369 A4868 A	*Choerolophodon*	*pentelici*	Maragheh	127,9
MA R - 2369 A4868 B	*Choerolophodon*	*pentelici*	Maragheh	126,4
MA R - 2371 / A4868?	*Choerolophodon*	*pentelici*	Maragheh	126,8
MA R - 2379 / A4826	*Choerolophodon*	*pentelici*	Maragheh	119,4
MA R - 2391	*Choerolophodon*	*pentelici*	Maragheh	114,8
MA R- 2447 A	*Choerolophodon*	*pentelici*	Maragheh	133,7
MA R- 2447 B	*Choerolophodon*	*pentelici*	Maragheh	123
NHM M 361	*Choerolophodon*	*pentelici*	Maragheh	123,2
NHM M 3957	*Choerolophodon*	*pentelici*	Maragheh	126,6
NHM M 7422	*Choerolophodon*	*pentelici*	Maragheh	126,3
TAL XXXI / A4831 /MAR.2392 LEFT	*Choerolophodon*	*pentelici*	Maragheh	123,6
TAL XXXI / A4831 /MAR.2392 RIGHT	*Choerolophodon*	*pentelici*	Maragheh	125,7
MA R - 2380	*Konobelodon*	*atticus*	Maragheh	99,6
MA R - 2395	*Konobelodon*	*atticus*	Maragheh	90,4
MA R - 2446 B	*Konobelodon*	*atticus*	Maragheh	67,2

1888 XII 21 K.4/E	*Deinotherium*	*giganteum*	Meidling	93
2000Z0028/0000 / SK2753	*Deinotherium*	*giganteum*	Meidling	92,8
A4319 / SK 2574 A	*Deinotherium*	*giganteum*	Mistelbach	71,7
A4319 / SK 2574 B	*Deinotherium*	*giganteum*	Mistelbach	82,4
1977/1048/0140	*Tetralophodon*	*longirostris*	Mistelbach	114,2
1977/1984/0137	*Tetralophodon*	*longirostris*	Mistelbach	123,8
2008Z0056/0001	*Tetralophodon*	*longirostris*	Mistelbach	80,2
1908NO.11 / SK 2758	*Deinotherium*	*giganteum*	Paasdorf bei Mistelbach	106,8
NHML M 7603	*Prodeinotherium*	*bavaricum*	Pontlevoy-Thenay	94,8
NHML M 7604	*Prodeinotherium*	*bavaricum*	Pontlevoy-Thenay	90,6
1835 IX 37	*Tetralophodon*	*longirostris*	Reichertshausen	111,1
1835 IX 42	*Tetralophodon*	*longirostris*	Reichertshausen	106,5
1835 IX 43	*Tetralophodon*	*longirostris*	Reichertshausen	113,2
932M	*Gomphotherium*	*angustidens*	Sacedon	112,6
934M	*Gomphotherium*	*angustidens*	Sacedon	106,5
NHML 37242	*Gomphotherium*	*angustidens*	Sansan	110,6
NHML 37242	*Gomphotherium*	*angustidens*	Sansan	108,9
NHML 37242 (DEXT.)	*Gomphotherium*	*angustidens*	Sansan	112,7
NHML 37242 (SIN.)	*Gomphotherium*	*angustidens*	Sansan	116,4
NHML 37243	*Gomphotherium*	*angustidens*	Sansan	115,7
NHML 40729 (DEXT.)	*Gomphotherium*	*angustidens*	Sansan	118,7
NHML 40729 (SIN.)	*Gomphotherium*	*angustidens*	Sansan	118,1
NHML 40730	*Gomphotherium*	*angustidens*	Sansan	112,9
NHML 40735	*Gomphotherium*	*angustidens*	Sansan	118,3
NHML M 10550	*Gomphotherium*	*angustidens*	Sansan	130,4
NHML M 10550	*Gomphotherium*	*angustidens*	Sansan	129
NHML M 10551	*Gomphotherium*	*angustidens*	Sansan	115,6
NHML 33520	*Prodeinotherium*	*bavaricum*	Sansan	81,2
1893 X 2P	*Gomphotherium*	*angustidens*	Simorre	98,8
NHML 32533	*Gomphotherium*	*angustidens*	Simorre	104,4
NHML 7425	*Gomphotherium*	*angustidens*	Simorre	90
NHML 33587	*Zygolophodon*	*turicensis*	St. Gaudens	86,15
NHML 33588	*Zygolophodon*	*turicensis*	St. Gaudens	93,6
NHML 33589	*Zygolophodon*	*turicensis*	St. Gaudens	97,7
2000Z0030/0000	*Deinotherium*	*giganteum*	Stratzing	102,8

114/1954	*Tetralophodon*	*longirostris*	Stratzing	105,4
336/1959	*Tetralophodon*	*longirostris*	Stratzing	120,6
575/ 1964	*Tetralophodon*	*longirostris*	Stratzing	106,4
604/1964	*Tetralophodon*	*longirostris*	Stratzing	81,5
LARGE JAW, UNNUMBERED	*Tetralophodon*	*longirostris*	Stratzing	101,5
SK2679	*Gomphotherium*	*angustidens*	Stratzing	115,6
2000Z0040/0000	*Deinotherium*	*giganteum*	Türkenschanze	83,1
1848 XXI 22 / SK2752	*Deinotherium*	*giganteum*	Wien 3	113,6
1828 XXXVII 4 /SK3059	*Tetralophodon*	*longirostris*	Wien-Belvedere	113
1848 X141 / SK 3086	*Tetralophodon*	*longirostris*	Wien-Belvedere	110,1
TA 7.19/1	*Tetralophodon*	*longirostris*	Wien-Belvedere	114,6
DISPLEY 2 A	*Deinotherium*	*giganteum*	Wienerbecken	107,1
DISPLEY 2 -B.	*Deinotherium*	*giganteum*	Wienerbecken	82,5
2000Z0023/0000	*Deinotherium*	*giganteum*	Wilfersdorf	104,9
2000Z0036/0000	*Deinotherium*	*giganteum*	Wilfersdorf	99,3
1841 XIII 5 / SK2761	*Deinotherium*	*giganteum*	Wilfersdorf	76,8
319M	*Gomphotherium*	*angustidens*	Villaluenga, Toledo	111,9
305M	*Gomphotherium*	*angustidens*	Villaobispo, Leon	109,6
331M	*Gomphotherium*	*angustidens*	Villaobispo, Leon	126,9
NHML 36754 (DEXT.) (CAST)	*Gomphotherium*	*angustidens*	Villefranche d'Astarac	115,5
NHML 36754 (SIN.) (CAST)	*Gomphotherium*	*angustidens*	Villefranche d'Astarac	118,4
NHML M 13995 (DEXT.) (CAST)	*Gomphotherium*	*angustidens*	Villefranche d'Astarac	114,2
NHML M 13995 (SIN.) (CAST)	*Gomphotherium*	*angustidens*	Villefranche d'Astarac	115,9
NHML 29632 (CAST)	*Prodeinotherium*	*bavaricum*	Villefranche d'Astarac	83,3
NHML 33590 (DEXT.)	*Zygolophodon*	*turicensis*	Villefranche d'Astarac	101,1
NHML 33590 (SIN.)	*Zygolophodon*	*turicensis*	Villefranche d'Astarac	92,8